THE FUNCTIONAL MORPHOLOGY OF THE MOUTHPARTS OF SOME
MOSQUITO LARVAE

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Homologies of the parts of the maxilla and the labium of mosquito larvae were studied. The name cardobasistipes is proposed for the triangular sclerite latero-posterior of the maxilla, previously known as the cardo or the palpifer. The numbers of serrations on the prementum and submentum were found to be of taxonomic value. The sequence of mouthpart movements of filter feeding and browsing species, and the progress of food particles from the feeding current into the mouth were observed. Differences in stiffness were found among the setae in different positions on the mouthparts. These differences were confirmed by staining the cuticle with Mallory's triple stain and are correlated with the functions of the setae during feeding. Flexible serrations at the tips of the labral brush hairs are used for raking food particles in most of the browsing species of Aedes and Culiseta studied. When in pond water neither the browsing nor the filter feeding larvae select the type of food they ingest. Feeding behaviour of the predatory larvae of Chaoborus americanus (Johannsen) and Mochlonyx velutinus (Ruthe) was observed.

INTRODUCTION

The mouthparts of a mosquito larva occupy a large portion of its head; their structure is degenerate. In this work emphasis is placed on the homologies of the parts of the maxilla and the labium, on the structure and function of the labral brushes and on the type and size of food particles ingested by the larvae.

The problems of homologies of the mouthparts did not occupy the early biologists who lacked adequate equipment for detailed study of minute structures. Hooke (1665) drew a mosquito larva, but he did not interpret all the parts of its anatomy accurately; for example, he labelled the external opening of the respiratory siphon as the anus. He further said about the "Water – Insect or Gnat": --"It is suppos'd by some, to deduce its first origin from the putrifaction of Rain Water. . ." He wrote that the larvae can move gently through the water by moving their mouthparts, and "eat" their way up through the water.

Reaumur (1738) described and illustrated the external features of a mosquito larva which seems to be a *Culex* species (*pipiens* according to Shannon, 1931). He gave an accurate description of the function of the labral brushes and described browsing and filter feeding activities of larvae.

The best known studies on mosquito larvae in the 19th century

are those of Meinert (1886) and Raschke (1887) who discussed larval morphology, function of mouthparts, and some of the habits of larvae and adults.

The names used by authors for the mouthparts of mosquito larvae are summarized in table 1. The following authors also referred to some mouthparts by specific names: Miall (1895), Johannsen (1903), Mitchell (1906), Puri (1925), Montchadsky (1945), and Cook (1956). A more complete list of literature on this subject is included in my thesis (Pucat 1962). It is evident that there is disagreement on the homology and nomenclature of certain mouthparts. There is less disagreement on the function of these parts, but this has not been studied exhaustively.

Classification of Feeding Habits

The structure of mouthparts, the method of feeding, and the habitat of the larvae are inter-related. On the basis of these factors culicine larvae have been classified into filter feeders, browsers, and predators (Surtees 1959).

It has been found convenient to follow this classification since it is based on morphological and functional characteristics. The criteria may be summarized as follows:

Filter Feeders - are larvae which strain out food particles from the water, such particles being sufficiently small to pass directly into the digestive tract without undergoing any further breakdown. Their salient morphological characters are: long, fine, unserrated labral brushes, large maxillae bearing many fine setae, small weakly chitinized mandibles, a weakly chitinized submentum possessing a large number of very small teeth and, associated with these features, large sub-apical tufts of setae on the antennae (Surtees 1959). These structural features were recognized by Wesenberg-Lund (1920) in several Danish species of mosquitoes. Nuttall and Shipley (1901) described in detail the function of the labral brushes of a filter feeder, an unnamed *Anopheles* species.

Feeding action similar to that observed by Nuttall and Shipley was also observed by Bekker (1938a, b) in *Anopheles maculipennis* Meigen, and by Renn (1941) in *Anopheles quadrimaculatus* Say and *Anopheles crucians* Wiedemann. Renn referred to the characteristic anopheline feeding method in which the floating particles are drawn straight towards the mouth as "interfacial" feeding. However, sometimes anopheline larvae employ a feeding method common to the larvae of other genera of mosquitoes in which the particles move in converging curved lines, and this Renn calls "eddy" feeding.

Browsers - abrade solid material, the particles of which require further manipulation by the mouthparts before entering the digestive tract (Surtees 1959). Mouthparts of this type have been described by Mitchell (1906), Howard, Dyar, and Knab (1912), Wesenberg-Lund (1920), Surtees (1959), Snodgrass (1959), Christophers (1960), and Clements (1963). All authors agree that browsing larvae are usually bottom feeders.

The labral brushes as well as the maxillary and mandibular bristles are shorter and stiffer than in the filter feeders. As Mitchell (1906)

pointed out, in brushing over debris at the bottom of a pool very long, slender hairs would be a disadvantage. Mandibles are used to manipulate any large particles that come into the feeding stream, and the submentum is used as a secondary grasping organ. The swimming position is usually at an angle of about 45° to the substratum. Morphological gradations occur between typical filter feeders and browsers (Wesenberg-Lund 1920, Surtees 1959).

Predators - have the labral brushes strongly chitinized. The role of the maxillae has been suppressed and the mandibles are the principal mouthparts. These are very large with strongly chitinized claws and take up most of the oral region of the head capsule. Associated with the strong claws are large, stiff spines which also aid in grasping the prey. This is true of the larvae of *Chaoborus* and *Mochlonyx* (Schremmer 1950, Peterson 1951, Cook 1956, and others). The submentum in all predatory species is well developed, the teeth being large and generally pointed. The increase in the strength of the submentum is associated with a reduction in the number of teeth and mouth brushes. Predatory larvae have large prehensile antennae which aid in grasping prey.

Evolution

Montchadsky (1937) has considered the environmental adaptation of larval and adult structures and behavioral characteristics important in classification. The type of feeding is a factor correlating the processes of evolution of larval and adult mosquitoes.

The Anophelinae and Culicinae have mostly plant-feeding larvae and blood-sucking adults (Montchadsky 1937, Hennig 1950). However, the Toxorhynchitinae and the culicine subgenus *Lutzia* have reversed their type of feeding; the larvae lead a predatory life, but have structures which indicate a previous adaptation to a vegetarian type of feeding. The adults of these mosquitoes either feed on plant juices (but carry traces of previous ability to suck blood), or appear to be optional blood feeders (Montchadsky 1937). In the Chaoboridae the adults are plant feeding while the larvae are predatory. Two lines of adaptation to predation are known: the surface film feeders such as *Eucorethra*, and the pelagic feeders such as *Chaoborus*.

In the initial stages of evolution of the mosquitoes either there was a change in the type of feeding of the adults (transition to blood feeding in the subfamily Culicinae), or of the larvae (the transition to predation in the Chaoboridae). According to Montchadsky (1937) these changes were provoked by certain changes in the nutritional requirements for the ripening of the sexual organs. If adequate food containing high quality protein is eaten by the predatory larvae, it is not then required to be eaten by the adults which may be vegetarian. On the other hand, non-predatory mosquito larvae do not obtain adequate high quality protein, so that the adults of these species must have it from the blood of vertebrates.

TABLE 1 - Summary of names which have been used for some mouthparts of mosquito larvae.

Author	Labral Area						Maxilla		Labium		
Meinert 1886 *C. annulatus*	clypeus	whirling organ	scutum of 1st metamere				internal lobe	external lobe			under-lip
Raschke 1887 *C. nemorosus*	upper lip	Strudel-apparat						maxilla			under-lip
Giles 1902 *A. rossi C. fatigans Mochlonyx Chaoborus*	labrum	whorl organ						maxilla			lower lip
Theobald 1901 *Anopheles Megarhinus*		whorl organ brush						maxilla			labial plate
Nuttall & Shipley 1901 *Anopheles*	clypeus	brush						maxilla			lower lip
Thompson 1905 *Culex*		flabella	palatum	flabellar inner retraction insertion	flabellar outer retraction insertion	epipharynx		maxilla	hypo-pharynx labium		mental sclerite
Imms 1907,1908 *Anopheles*	clypeus	brush	palatum	chitinous apodeme of epipharynx		epipharynx		maxilla	hypo-pharynx		labial plate
Wesché 1910 *Culex*	brush							maxilla	labium (pre-mentum)		lower lip
Howard 1912 *Culex Aedes Anopheles*	labrum	mouth brush flabella	palatum	apodeme		epipharynx		maxilla	labium hypo-pharynx	mental sclerite	hair fringed plate
Wesenberg-Lund 1920 *Culex Culiseta Aedes*	labrum	flabella	palatum	apodeme				maxilla	labium hypo-pharynx	mental sclerite	hair fringed plate
Salem 1931 *A. fasciatus*	labrum	feeding brush	palatum	apodeme	clypeo-labral suture	epipharynx	first segment of palp	maxilla	labium	mentum	
Bekker 1938	clypeus	flabella	antero longitudi-		transverse	epipharynx		maxilla	labium		sub-mentum

	labrum	labral brush	palatum	messor	messorial apodeme	palatal bar	stipes	palpifer	pre-mentum	sub-mentum	aulaeum
Cook 1944, 1949 *Culiseta incidens*	labrum	labral brush	palatum	messor	messorial apodeme	palatal bar	stipes	palpifer	pre-mentum	sub-mentum	aulaeum
Matheson 1944 *Anopheles*	labrum	mouth brush	palatum				maxilla		pre-mentum	mentum	mentum
Farnsworth 1947 *A. quadrimaculatus*	labrum	labral brush	median labral brush	messor	messorial apodeme	palatal bar	maxilla		hypopharyngeal body	inner tooth of mentum	outer tooth of mentum
Schremmer 1949 *A. maculipennis*	labrum					epipharynx Apparat	maxilla			labium	
Chaudonneret 1951 *C. pipiens*	labrum		labrum	messor		epipharynx	maxilla				
Foote 1953 *C. peccator C. atratus*	labrum	mouth brush		messor		palatal bar	maxilla		pre-mentum	mentum	aulaeum
Shalaby 1957 *Aedes Culex Culiseta*	pre-clypeus	lateral labral brush	palatum	labral brush apodeme	posterior apodeme	epipharyngeal sclerite	lacinia galea cardo - stipes	palpifer	hypopharynx	para-glossa	glossa
Menees 1958 *A. quadrimaculatus*	labrum	mouth brush	median brush	torma	anterior intertormal bar	posterior intertormal bar	lacinia galea stipes	cardo	labio-hypopharyngeal body	inner tooth of mentum	outer tooth of mentum
Snodgrass 1959 *Aedes Culex Culiseta Anopheles*	labrum	lateral feeding brush / mouth brush	median brush	torma	apodeme	epipharyngeal bar	stipes	cardo	labium hypopharynx	hypostomium	aulaeum
Surtees 1959 *Culex Aedes*		mouth brush					maxilla		mentum		
Christophers 1960 *A. aegypti*	pre-clypeus	flabellum	palatum	apodeme	stirrup apodeme	epipharynx	distal part of maxilla	palpifer	labium hypopharynx	mental sclerite	
Jones 1960 *A. quadrimaculatus*	labrum	lateral labral brush		messor		palatal bar	maxilla		pre-mentum	mentum	sub-mentum
Present work	labrum	lateral labral brush	median labral brush	torma	posterior tormal apodeme	epipharyngeal bar	lacinia disti-stipes	cardo basistipes	pre-mentum	mentum	sub-mentum

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Thompson 1905 *Culex*		flabella	palatum	flabellar inner retraction insertion	flabellar outer retraction insertion		epipharynx	maxilla		hypopharynx labium	mental sclerite	
Imms 1907, 1908 *Anopheles*	clypeus	brush		chitinous apodeme of epipharynx			epipharynx	maxilla		hypopharynx	labial plate	
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Salem 1931 *I. fasciatus*	labrum	feeding brush	palatum	apodeme		clypeo-labral suture	epipharynx	maxilla	first segment of palp	labium	mentum	sub-mentum
Dekker 1938	clypeus	flabella	antero median ...	longitudinal lever		transverse ...	epipharynx	maxilla		labium	mentum	sub-mentum
Marshall 1938 *Aedes Culex Anopheles*	pre-clypeus	mouth brush	labrum				epipharynx	maxilla		hypopharynx	mentum	sub-mentum
Cook 1944, 1949 *Culiseta incidens*	labrum	labral brush	palatum	messor	messorial apodeme		palatal bar	stipes	palpifer	pre-mentum	sub-mentum	aulaeum
Matheson 1944 *Anopheles*	labrum	mouth brush	palatum					maxilla		pre-mentum	mentum	
Farnsworth 1947 *I. quadrimaculatus*	labrum	labral brush	median labral brush	messor	messorial apodeme		palatal bar	maxilla		hypopharyngeal body	inner tooth of mentum	outer tooth of mentum
Schremmer 1949 *I. moralipennis*	labrum						epipharynx Apparat	maxilla			labium	
Chaudonneret 1951 *C. pipiens*	labrum		labrum	messor			epipharynx	maxilla				
Foote 1953 *C. precator C. unatus*	labrum	mouth brush	mouth brush	messor			palatal bar	maxilla		pre-mentum	mentum	aulaeum
Shalaby 1957 *Aedes Culex Culiseta*	pre-clypeus	lateral labral brush	palatum	labral brush apodeme	posterior apodeme	transverse bar	epipharyngeal sclerite	lacinia galea cardo - stipes	palpifer	hypopharynx	para-glossa	glossa
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Present work	labrum	lateral labral brush	median labral brush	torma	posterior tormal apodeme	transverse bar	epipharyngeal bar	lacinia disti-stipes	cardo basistipes	pre-mentum	mentum	sub-mentum

MORPHOLOGY OF THE HEAD AND MOUTHPARTS OF MOSQUITO

LARVAE

The mouthparts of mosquito larvae were compared with the mouthparts of larvae of other Nematocera, Mecoptera, and other panorpoid groups, or with published descriptions of them.

Procedures

Two species of mosquito, *Aedes aegypti* (L.) and *Culiseta inornata* (Williston) were reared in the laboratory, so that fresh specimens of these species were almost always available.   Rearing methods of Trembley (1955) and McLintock (1952) were followed. Specimens from the field were also observed alive and dissected in the laboratory. Since larvae were available in abundance, dissected heads were mostly studied. The dissections were done in glycerine. Hoyer's mounting medium and neutral Canada Balsam were used for mounting the mouthparts. Eosin-water solution was used for staining dissected muscles, and modified (Peterson 1960) Mallory's triple stain for larval head cuticle.   The mouthparts were boiled for 15 minutes in an 8% aqueous solution of KOH before staining.

Manton (1958) commented on the staining reaction of cuticle with Mallory's. She concluded that sclerotized non-staining exocuticle is unstretchable when thick, that orange and red-staining cuticle are progressively less fully sleerotized, less rigid, and more elastic than the non-staining cuticle, and that blue-staining cuticle is fully flexible, more stretchable, but less elastic.

The structure of the heads of the larvae of *Aedes fitchii* (Felt and Young) and *Culiseta inornata* was studied in detail, and other species (table 2) were compared with them. Larvae of a *Chironomus* species, and of *Mochlonyx velutinus* (Ruthe) and *Chaoborus americanus* (Johannsen) were also examined.

The Head Capsule

The largest sclerite in the head capsule of a mosquito larva is the frontoclypeus, which extends over most of the head surface dorsally. The genae are lateral, the postgenae postero-lateral; they extend ventrally to complete the head capsule (figs 1, 2). The median ventral part of the united postgenae, posterior to the mouth, has been given various names.   I consider it as the subgena.   It is bounded by two lines of cuticular thickening ridges which are known variously as the submental-postgenal sutures (Shalaby 1956 and 1957a, b, c, d) hypostomal sutures (Menees 1958a, Christophers 1960), and thickening ridges (Snodgrass 1959).   I agree with Snodgrass' interpretation of the homologies of the ventral head sclerites. In homologizing these sclerites of the mosquito larva Snodgrass digresses to discuss the ventral head sclerites of other insects, especially insects in which a trend toward a ventral elongation of the postgenae is evident. As examples he cites certain beetles in which the entire labium with a gular addition to the submentum is enclosed between the postgenae.   He states, however, that this condition is not
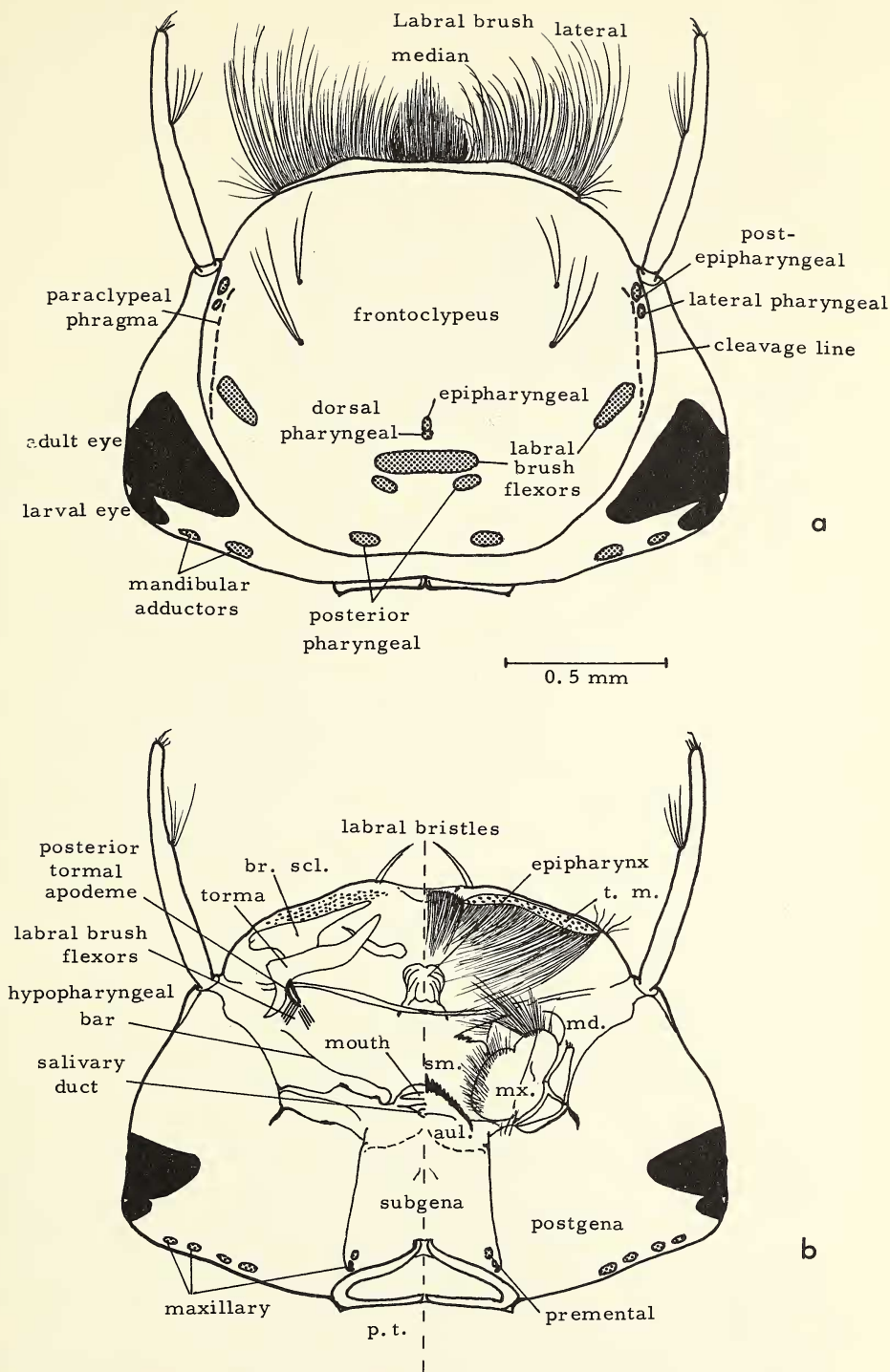
Fig. 1. The head of *Aedes fitchii* (F. & Y.) larva, (a) dorsal view showing muscle origins and extended labral brushes, (b) ventral view with brushes retracted and mouthparts removed from right hand side. mx. maxillae, md. mandible, sm. submentum, t.m. tessellated membrane, aul. aulaeum, p.t. posterior tentorial pit. Muscle attachments stippled.
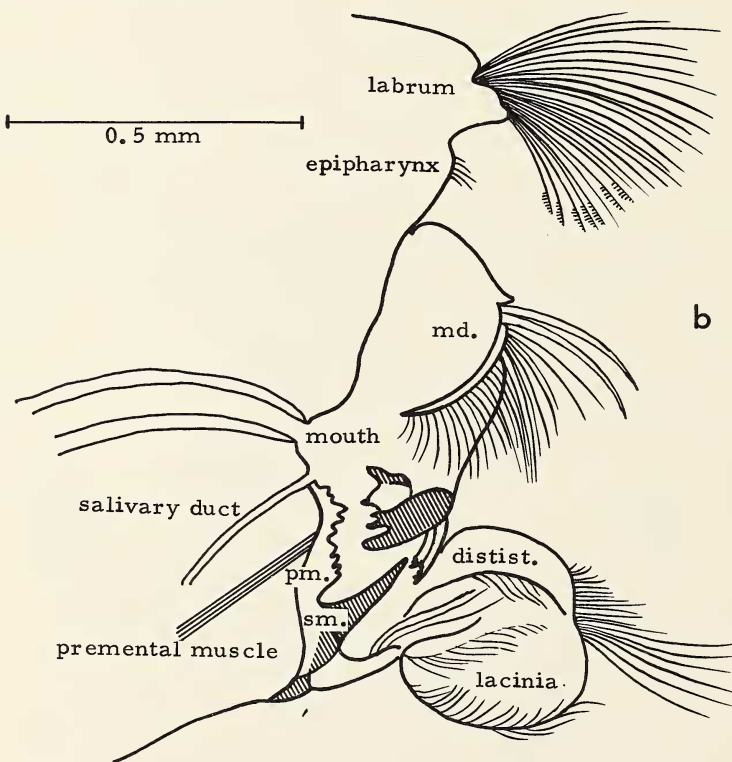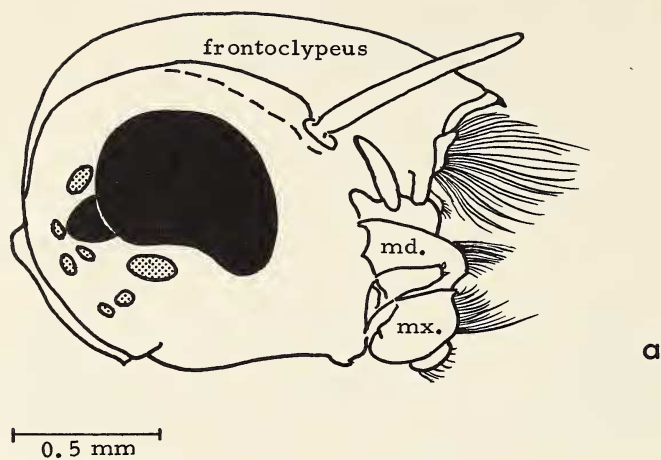
Fig. 2. (a) Lateral view of the left side of the head of *Aedes fitchii* (F. & Y.) larva. (b) Sagittal section through the mouthparts of *Aedes fitchii* larva. md. mandible, mx. maxillae, pm. prementum, sm. submentum, aul. aulaeum, distist. dististipes. Muscle attachments stippled.

represented in mosquito larvae. More commonly, the postgenae come together medially and displace the labium. A final stage in the displacement of the labium is seen in the larvae of Chironomidae where the labium has become greatly reduced and is hidden from below by a median hypostomal lobe of the united postgenae.

A similar process of closure and elongation of the postgenae and reduction of the labium occurs in nematocerous larvae as discussed by Anthon (1943), Hennig (1948, 1950, 1952), and Snodgrass (1959). In the larvae of the primitive rhyphid *Olbiogaster* the small postgenal lobes are posterior to the submentum of the labium (Anthon 1943). In tipulid larvae, described by Vimmer (1906) and other authors, as well as in other nematocerous larvae the genae are completely united ventrally and the labium is dorsal to the subgenal lobe. In the mosquito larva, to distinguish the central area between the thickening ridges of the genae Snodgrass (1959) named it the subgena, and the areas laterad of the ridges the postgenae. I use this nomenclature.

Cook (1944a, b, 1949), following Ferris's (1947) and Henry's (1947) theories of the segmentation of the arthropod head, considered the postgenae and the subgena as parts of the maxillary segment. Shalaby (1957) considered the apical part of the subgena as the mentum and the remainder as the submentum. As evidence for this idea Shalaby referred to Wheeler's (1893) embryological work in which the latter observed that the rudiments of the second pair of maxillae on the sides of the embryonic body give rise to the labium in the embryos of the locust *Xiphidium ensiferum* Scudder, in *Gryllus luctuosus* Serville, and in *Stagmomantis carolina* (Johannsen). Shalaby believed that the median suture present on the ventral sclerite of the head of *Culex molestus* Forsk. larva is due to incomplete fusion of the embryonic rudiments of the second maxillae. That the embryonic second maxillae give rise to the labium has been shown by Butt (1957) in *Oncopeltus fasciatus* (Dallas), and by other authors in other insects. Christophers (1960) also believes that the subgena is the labial area; he homologizes the subgenal and postgenal areas posterior to the maxillae with the fused bases of the maxillae (cardo and stipes). He thus believes that in the larval as in the adult stages of mosquitoes the bases of the maxillae extend to the occipital foramen, forming the hypostomal area. However, the sclerite which Christophers considers as the base of the maxilla serves as the origin of pharyngeal, mandibular, and maxillary muscles which in most other insects originate on the tentorium or on the cranial wall (Snodgrass 1935). In the adult *Aedes vexans* (Meigen) the maxillary muscles originate on the tentorium (Peterson Hoyt 1952). On the other hand, none of the postgenal muscles of the mosquito larva originates on the tentorium. If the larval postgena and subgena are to be considered as the fused maxillary cardo and stipes, then the origins of the various muscles upon them are difficult to explain. Menees (1958a), studying the embryonic development of *A. quadrimaculatus*, observed that the median suture on the ventral head sclerite in this species is the result of incomplete fusion of the postgenae.

Most sutures which are characteristic of the primitive insect head are absent from the heads of mosquito larvae. Two cleavage lines extend anteriorly from a short posterior occipital stem (fig 1). These

cleavage lines may be homologous with the frontal sutures and the epi-
cranial suture of other insects. However, Snodgrass (1947, 1958) and
DuPorte (1953) state that the frontal arms of this suture follow diverse
paths in different insects, and therefore do not define any specific part
of the head. For this reason, in this work head sclerites and mouthparts
have been named in reference to muscle origins.

Approximately in the center of the frontoclypeus arise the labral
and epipharyngeal muscles (fig. 1) which usually originate on the clypeus,
and posterior to these are the origins of the pharyngeal muscles which
generally occur on the frons. In the head of *Aedes fitchii* (Felt and Young)
larva and in all the other mosquito species examined, there is no
demarcation between the areas where the different muscles originate.
According to DuPorte (1962) in some insects the boundary between
the clypeus and frons, in the absence of an epistomal suture, is fixed
by the position of the anterior tentorial pits. In the heads of mosquito
larvae, however, the epipharyngeal muscle (usually on the clypeus) orig-
inates much posterior to the anterior tentorial arms.

The tentorium in the mosquito larva is represented by anterior
and posterior arms. The anterior arms originate on the head capsule
medial to the antennae, in the same area where the hypopharyngeal bars
arise (fig. 1). The long, slender anterior tentorial arms connect to the
short posterior arms on the postero-ventral part of the head. There
is no tentorial bridge.

On each side of the head a hypopharyngeal bar connects the
hypopharynx to the side of the cranium (fig. 1).

The Labrum

The labrum of the larva of *Aedes fitchii* consists of a narrow
transverse sclerite dorsally (fig. 1). Ventrally it is composed of a
membranous area to which three brushes are attached, one median
and two lateral and movable. The median brush is connected to each lateral
labral brush and to the distal part of the dorsal labral sclerite by a
membrane which has ben variously named. In the larvae of *Lutzia halifaxi*
Theobald, Cook (1944b) referred to it as a "pennicular area..beset
with small oval pits arranged in definite rows." Because of its appear-
ance Christophers (1960) called it the tessellated membrane, and this
is the name adopted here (fig.5). However, this name does not describe
the membrane accurately in all the larvae that I examined. This is
discussed further below.

In both *A. aegypti*, (Shalaby 1957a) and *Aedes fitchii*, two types of
hairs are found on the median brush; long thin branched hairs posteriorly,
and short stout hairs with serrated distal ends anteriorly. Both types
are shorter on the sides of the brush than medially.

The lateral labral brushes are composed of three types of hairs
which differ in length, thickness, curvature, and location. The hairs of
the first type are simple, relatively short, thin, soft, without definite
curvature, and are located postero-laterally, dorsally, and ventro-
medially overhanging the pharynx (figs. 1, 3). These hairs, which are
attached to the tessellated membrane, do not take part in creating a
feeding current. Hairs of the second type are long, simple, thin,

slightly curved at their bases and at their distal ends, and are located
in the lateral posterior two thirds of the brush (fig. 3). Anterior to
them are hairs of type three. Types two and three take an active
part in creating currents. The apices of type three hairs are provided
with serrations (17 - 20 per hair). The serrations on the lateral type
three hairs are smaller and slightly closer to each other than those
on the more medial hairs.

Three types of hairs were found in all the browsing species of
Aedes and *Culiseta* except in *Aedes cinereus* Meigen and *A. canadensis* (Theo).
which have only short, simple hairs on their lateral brushes. When the
labral brushes are stained with Mallory's the bases of all the hairs stain
red. Next above the bases a narrow layer of blue appears across the
hairs and above this layer hairs of type one and two stain red to their
tips. Hairs of type three stain partly red above the blue portion but
they stain blue apically, in their serrated regions. A large proportion
of the most median type three hairs stains completely blue above the
red bases. In *A. fitchii* and the other *Aedes* larvae, as well as in the
browsing *Culiseta* larvae that were examined, the apices of hairs of types
one and two are tapered. Also tapered are the apices of all the hairs
of the labral brushes of the filter feeders, *Culiseta morsitans* (Theo.) and
Culex territans Walker. In the brushes of the filter feeding larvae all
the hairs are simple. They all have red-staining bases, blue-staining
portions above the bases, and red-staining middle and apical portions.
In the filter feeding larvae a large group of hairs, originating medially
on each lateral labral brush, overhangs ventrally, partly covering the
epipharynx. A smaller number of simple hairs extends in this position
in the browsing larvae (fig. 1). In all the larvae that were examined these
hairs are red - staining. In the larvae of *Chaoborus americanus* the labral
brushes consist of a few hard, short, brown bristles on the small sclerite.
In the larva of a *Chironomus* species examined a few labral bristles are red-
staining and the remainder are blue-staining. Thus the staining reaction
of the labral brushes of the filter feeding and browsing larvae indicates
that their hair bases are elastic and the portions above the bases are
flexible. Flexibility of these hairs was seen when larvae were observed
feeding and also when the hairs were deflected with a needle.

In the mosquito larvae examined all the hairs of the lateral brushes
except type one are attached to sclerotized rods which extend transversely
across the basal area of the brush (figs. 3 and 4). Salem (1931) seems to
be referring to these rods in *Aedes fasciata* (Fab.) (*A. aegypti* L.) when
he states that the chitin of the labral brush "exhibits a peculiar striated
appearance." Christopher's term for these rods, "cross bars," is used
here. On each lateral labral brush of *A. fitchii* larvae between forty-
five and fifty of these bars are present and each bears approximately
twenty hairs. Thus each lateral brush contains nearly a thousand hairs.
A similar number of hairs is present in each lateral brush of *C. inornata*
larvae.

The cross bars are cuticular thickenings of the tessellated mem-
brane (fig. 5) with their dorsal ends free in this membrane next to the
dorsal sclerite of the labrum. When the cross bars are torn away from
the tessellated membrane and the hairs, depressions on them where the
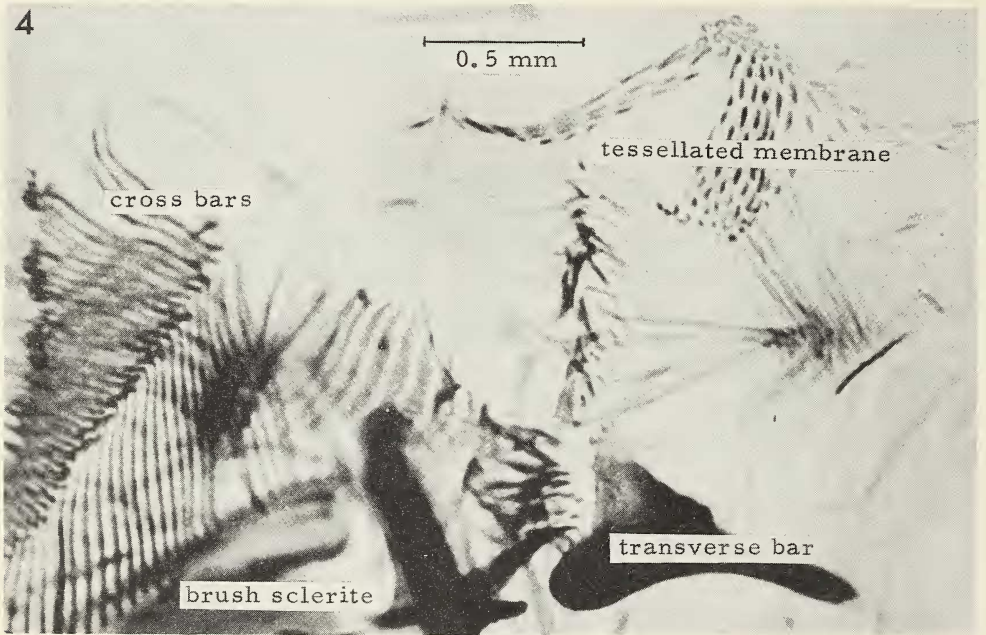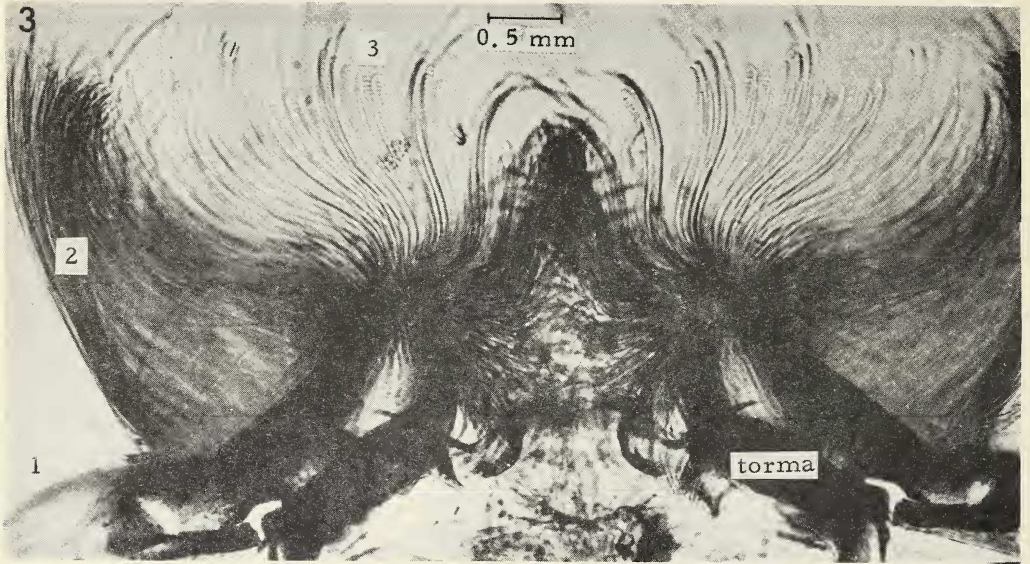
Fig. 3. Ventral view of the labrum of the larva of *Aedes fitchii* with the lateral labral brushes extended. Numbers indicate hair types.

Fig. 4. Details of labral hair attachments of the larva of *Culex territans*.
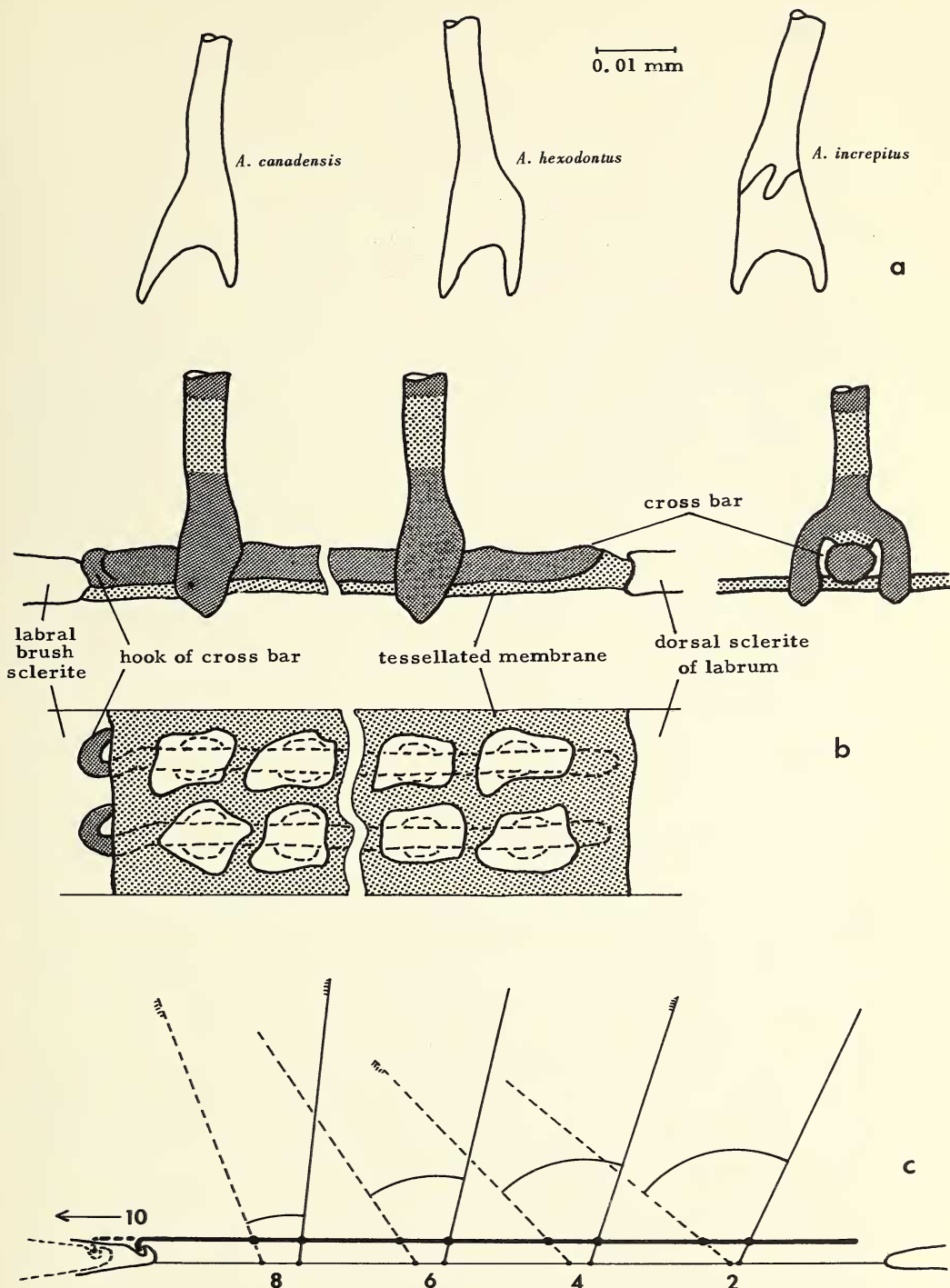
Fig. 5. (a) Forked bases of labral hairs of *Aedes* larvae; anterior views. (b) The relationship between hair base, cross bar, and the tessellated membrane, and the holes and depressions left in this by the removal of hairs and cross bars. Open stipple stretchable cuticle (stains blue); close stipple, flexible but relatively non-stretchable cuticle (stains red). (c) Diagram showing how the hairs are brought together by the increasing angle of movement at greater distances from the brush sclerite, because of differential stretching between the cross bars and the tessellated membrane.

hairs were attached can be seen. The other end of each cross bar is curved into a hook; it terminates in the brush sclerite which is roughly triangular and is attached to the median part of the torma by an apodeme (fig. 3). Muscles that move this sclerite are inserted on the posterior tormal apodeme (fig. 1). When the hairs are pulled off the membrane, their forked bases, the cross bars, and part of the membrane comes with them. This leaves holes in the membrane and confirms that the cross bars are more strongly attached to the hair bases than to the membrane. The hole may be rhomboid, square, pentagonal, hexagonal, oval, or roughly circular and form a mosaic pattern on the membrane which gives it its names. The cross bars leave depressions in the tessellated membrane.

When this complex is stained with Mallory's the cross bars and the hair bases stain red indicating rigidity, while the tessellated membrane and small parts of the hairs above their bases stain blue, indicating stretchability. The edges of the holes may be outlined in red perhaps because of some change in the character of the material of the membrane resulting from tearing.

The ends of the epipharyngeal bar are attached to the posterior parts of both tormae (figs. 1, 3). At the anterior end of each torma a narrow sclerite projects medially. These sclerites are known as transverse bars (Shalaby 1957a) or palatal bars (Christophers 1960). Their structure in *A. fitchii* is slightly different from that in *A. aegypti* as described by the above authors. The bars of *A. aegypti* are slender and from each a small curved sclerite projects anteriorly. In *A. fitchii* they are stout and curved medially, and are attached by thin sclerites to the tormae. In *Culex territans* the bars are straight and have wide basal parts.

In the species examined only the posterior apices of the tormae stain blue; the remainder of these structures with their apodemes retain their brown color. Thus the tormae and their apodemes are rigid, highly sclerotized structures. The associated membranes stain light blue.

The labrum of the predatory *Chaoborus americanus* larva is greatly reduced; it lacks brushes but possesses a few short stiff bristles at the tip of the labral sclerite (Cook 1956). These bristles stain dark red.

The Epipharynx and Preoral Cavity

The epipharyngeal apparatus lies between the posterior ends of the tormae and combs food particles from brushes to the mandibles. Schremmer (1949) called it the "Epipharynx-apparat" because it is musculated and has an active rather than a passive function.

The structure of the epipharynx in the species examined is very similar to that described by Shalaby (1957) and Christophers (1960) in *A. aegypti*. In *A. fitchii* and the other browsers the hairs are coarser than in *Culiseta morsitans* and *Culex territans*. The spines and hairs stain dark red in *A. fitchii* which indicates medium hardness; they stain lighter red in *C. morsitans* and *C. territans* and are probably softer in these species. The epipharyngeal bar stains medium blue in all specimens. That this flexible structure can move anteriorly and posteriorly has been observed in living larvae of *A. aegypti* and *C. territans*

The post-epipharyngeal area consists of a membrane between the epipharynx and the pharynx. It is similar to that described by Cook (1944b) in *Theobaldia incidens* (= *Culiseta incidens*). Two pairs of muscle strands originate on the frontoclypeus, one of these forks before its insertion in the membrane between the epipharynx and the pharynx. Since these muscle strands have a common origin on the cranium medially of the antenna (fig 1), I consider them as fascicles of one muscle, the postepipharyngeal.

The Mandibles

The mandibles of mature *Aedes fitchii* larvae consist of flattened, roughly quadrilateral lobes with their mesal ends produced into strongly sclerotized toothed processes and lower seta-bearing lobes. They are similar to the mandibles of most culicine larvae which have been described by other authors.

On the mesal margin of each mandible is found a fringe of pigmented, long, mesally directed setae with stout bases and sharp points. Shalaby (1957a) called this fringe the mandibular comb when he described it in *A. aegypti* . The number of the curved, stout and sharply pointed setae varies in fourth instar larvae of the species that I examined. Eleven were usually found in *A. fitchii* , nine in *C. inornata* , and fifteen in *A. aegypti* . Another series of setae extends meso-dorsally from the dorsal side of the mandible, medially of the large lateral bristles; this series Shalaby names the mandibular brush. In *C. inornata* it usually consists of 40 setae; in *A. fitchii* of 54. The number of lateral bristles is variable between species, but constant in all the species seen; in *A. fitchii* two are present and in *C. inornata* three. When the mandibular brush and comb setae of the *Aedes* and the *Culiseta* browsing species are stained with Mallory's their bases stain blue, and thus are soft; the remaining parts stain dark red, and are harder. The mandibular setae of the filter-feeding species , *Culiseta morsitans* and *Culex territans* are softer than those of the browsing species. The lateral bristles remain brown in all the species examined. All the mandibular bristles and setae in the mandible of *Chaoborus americanus* stain dark red or remain brown.

The number of teeth in *A. aegypti* , as described by Shalaby, is similar to that in *A. fitchii* and to the other *Aedes* species that were examined. The number of ventral teeth in *C. inornata* is similar to that found in the browsing *Aedes* species, but dorsally only three teeth are present in *C. inornata* whereas five are present in all specimens of all the *Aedes* species. The extent of heavy sclerotization in the tips of the mandibles, mainly the teeth, is approximately the same in *C. inornata* and the browsing *Aedes* species. The heavily sclerotized area is smaller in the filter feeders, and it is largely extended in the predatory *Chaoborus americanus* and *Mochlonyx velutinus* . These characteristics agree with the characteristics of browsers, filter feeders, and predators that Surtees (1959) discusses. Medially, on the dorsoventral ridge of the mandible a group of long spines reaches the anterior part of the pharynx. Schremmer (1949) discusses the function of similar spines on the mandible of *Anopheles maculipennis*. Anterior and posterior mandibular articulations are indicated in fig. 1.

The Maxillae

Each maxilla of *A. fitchii* (fig. 7) consists of a rectangular flattened lobe which bears a brush of long hairs apically, and a series of three rows of short hairs medially in an area demarcated by a suture on the oral (dorsal) side. Proximal to the palpus is a triangular sclerite about half the width of the main lobe, which is attached to these structures and to the post gena by a membrane. This sclerite bears a spine medially. Baso-ventrally the maxillary palpus bears sclerotized processes which articulate with a postgenal articular process inside the head (fig. 1). The mandible also articulates with the postgena and the maxilla at this point. Two muscles are inserted in the center of the main maxillary lobe; a single strand originates on the subgena mesally to the posterior tentorial pit, and a double strand originates on the postgena posterior to the eye (fig. 1).

To decide what parts of the maxilla of *A. fitchii* larvae are homologous with parts of maxilla of other insects, the relation between sclerites and musculature must be considered. It is generally accepted that as Imms (1944) states ". . . the Mecoptera are the nearest living representatives of ancestors of Diptera. . . " This view is also expressed by Applegarth (1939), Ferris and Rees (1939), Potter (1948), Hinton (1958), and others. We should therefore look for homologies of the maxilla of the mosquito larva in the Mecoptera and in other members of the suborder Nematocera. The palpus is the only structure on the homology of which all the authors agree. Since the palpus is connected to the base of the main maxillary lobe, and since the palpus in all insects is connected to the stipes, it seems logical to consider this lobe as the stipes. According to Snodgrass (1936) and Das (1937) the stipes can be distinguished by the origin of the muscles of the palpus. However, this criterion does not apply when the palpal muscles are absent as from mosquito larvae and larvae of *Tipula* and *Bibio* as described by Das (1937) and Cook (1944a). The two muscles that are present in this structure are probably the cranial flexors of the stipes (rather than of the lacinia). The double strand which originates on the postgena is one of these, and the adductor of the stipes which usually originates on the tentorium is the other. In the culicid larva the origin of the latter has shifted to the subgena.

Snodgrass (1935) and Das (1937) hold that the lacinia has a cranial flexor and the galea has only a stipital flexor in larval and adult stages of many insects. Das also states that many larvae lack the flexor of the galea, but when the lacinia is present its cranial flexor is always retained. The same author adds that the cranial flexor of the lacinia plays an important role in the interpretation of the lobes. No trace of stipital flexor was found in any culicid larva examined. The only cranial flexor present is inserted so close to the median side of the main lobe that it is almost on the bristle-covered area which is demarcated by a suture on the oral side of the lobe (fig. 7). Furthermore, this median bristly area functions as a lacinia. Therefore I agree with Shalaby (1957a, 1958) that this part of the maxilla is the lacinia, and that the cranial flexor of the lacinia now functions as a stipital flexor.

In the larvae of *Panorpa* both galea and lacinia are present (Das 1937); in *Apterobittacus* only the lacinia is present in the larval stage and the galea appears in the pupal stage (Applegarth 1939); in both *Tipula* (Das 1937) and *Bibio* (Cook 1944b) only the lacinia is present in the larval stage. The
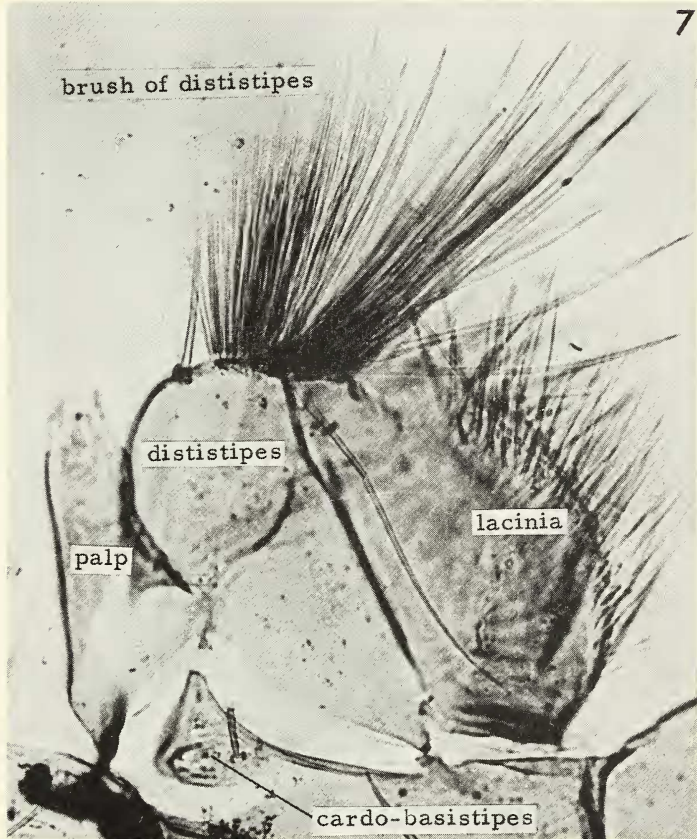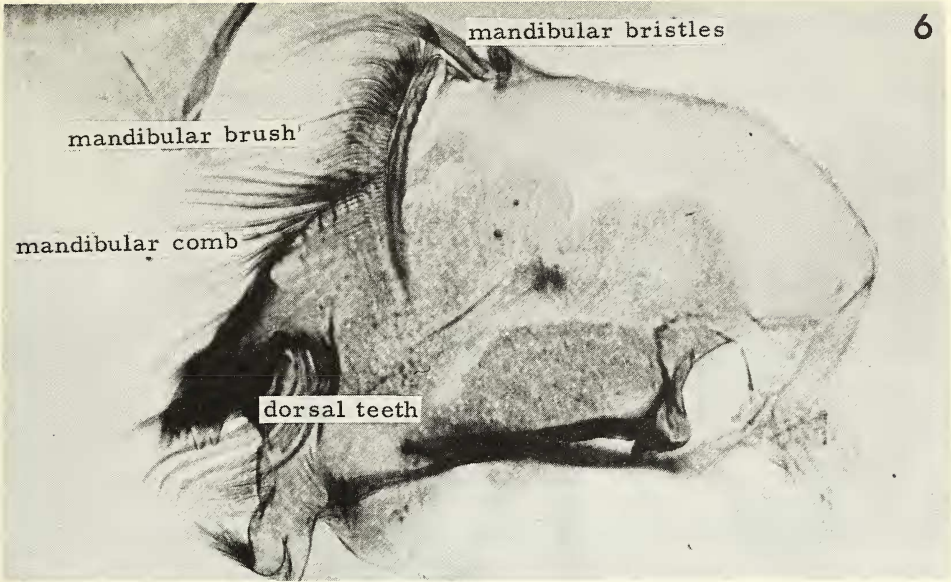
0.5 mm

Fig. 6. Ventral view of the left mandible of mature larva of *Aedes fitchii*
Fig. 7. Dorsal view of the left maxilla of mature larva of *Aedes fitchii* .

triangular sclerite which is considered as the palpifer by most authors
I believe to be at least a partial vestige of the cardo. In the larva of
Panorpa the cardo has a relative size, shape and position similar to that in
the mosquito larva, and it also lacks musculature (Das 1937). In the lar-
vae of each of *Apterobittacus*, *Bibio*, and *Tipula* species the structure named
as cardo by the respective authors, is proportionately larger than in the
larvae of *Aedes*, *Culex*, and *Culiseta*. In the former three larvae the so-
called cardo extends posterior to the stipes and the palp. If this structure
is homologous with the triangular sclerite in the mosquito larva then this
sclerite must be the cardo and not the palpifer. However Hinton (1958)
points out that the stipes is divided into a basistipes and dististipes in all
the Panorpoidea except the more specialized Diptera. The same author
further states that failure to recognize the fact that the stipes is sub-
divided in primitive forms of all recent orders of the Panorpoidea has
resulted in the misidentification of the dististipes as the palpifer. Hinton
also states: "in the Panorpoidea in which the cardo has become fused to
the basistipes the combined structure which may be called the cardostipes
has almost without exception been identified as the cardo and the disti-
stipes as the stipes. For instance, the cardo plus basistipes of *Bibio* is
called the cardo and the dististipes is called the stipes by Imms (1944) and
Cook (1949)..." In the light of Hinton's statements then I consider the
triangular sclerite of the mosquito larval maxilla as homologous with
the fused cardo and basistipes. The main maxillary lobe is the disti-
stipes plus the lacinia. In addition Hinton mentions that within the
Nematocera a fusion of the cardostipes with the dististipes takes place for
example in the Culicidae, but he does not specify in what group of the
Culicidae. He may be referring to the genus *Anopheles*, for in that genus
there is no triangular sclerite proximal to the maxillary palp and the
dististipes as in the genera *Aedes*, *Culex*, and

  Essentially the same structural arrangement of the maxilla
was found in all the *Aedes*, *Culex*, and some *Culiseta* larvae that I
examined. Some difference from the browsers was found in the shape
of the maxillae of *Culex territans*, *Culiseta morsitans*, *Aedes canadensis*, and
A. cinereus Each maxilla in these species is cone-shaped, wide at the
base and narrow at the apex where a brush of simple hairs is attached.
The maxillae of most browsers are similar in shape to those of
Aedes fitchii. Between the browsers and filter feeders differences occur
in the number and length of hairs on the distal end of the dististipes and
on the lacinia. In the maxillae of both filter feeders and browsers the
apical brush hairs of the dististipes are longer than the lateral hairs of
the lacinia, and in the filter feeders all these hairs are proportionately
longer than in the browsers. The longest maxillary hairs in *Culex territans*
and *Culiseta morsitans* are approximately one and a half times as long as
the dististipes; whereas the homologous hairs in *A. fitchii* and the other
Aedes browsers are only approximately as long as the dististipes, and
in both *Culiseta inornata* and *C. impatiens* (Walker) they are half the length of
the dististipes. The maxillary brushes of the browsing *Aedes* species are
composed of more hairs than those of the filter feeding species. The
maxillae of *C. inornata* and *C. impatiens* larvae have brushes consisting
of very few hairs, thus resembling the maxillae of predatory larvae.

Another similarity of the maxillae of these two *Culiseta* species to the predatory larval maxillae is the fusion of the palps with the cardobasistipites.

With Mallory's stain the bases of the maxillary brush hairs of browsing larvae stain blue and the remaining parts red, but the whole hairs stain blue in filter feeders. Thus the maxillary brushes of browsers are stiff, a feature of obvious value in their activity.

The short medial bristles of the lacinia are arranged in three rows in all the species that I studied; they are more numerous in browsers than in filter feeders. These hairs are longer in *A. fitchii* and the other *Aedes* browsers than in *C. inornata* and *C. impatiens*. In all the browsers these hairs stain red, indicating moderate stiffness. The hairs of the lacinia of the filter feeders stain blue and thus are soft.

The Labium and Hypopharynx

I consider the labium of the larva of *A. fitchii* to consist of the prementum and the submentum. This view is in agreement with Cook's (1944b) interpretation for other genera. The prementum (fig. 2) is a rectangular membranous area bearing a series of serrated sclerites and papillae, and is situated between the hypopharynx and the mouth opening dorsally, and the triangular serrated submental plate ventrally.

Dorso-ventrally two long sclerites extend through the centre of the prementum and dorsally terminate ventral to six small serrated sclerites which project ventrally from the membranous base. On the sides of the membrane three serrated plates are situated ventrally. These three plates are connected to each other, and dorsally to the small central serrated sclerites. Each plate has a different number of serrations, which vary in different species. In *A. fitchii* the dorsal plate has four serrations, the median plate nine, and the ventral plate five. Six larvae of each of two closely related species, *Aedes hexodontus* and *A. punctor* were also examined, and the average numbers of serrations were found to be: dorsal plate 5 serrations in *A. hexodontus*, 4 in *A. punctor*; median plate 6 in *A. hexodontus*, 9 in *A. punctor*; ventral plate 6 in *A. hexodontus*, 10 in *A. punctor*. This may be a useful taxonomic character for separating closely related species. Considerable care is required in preparing the slides if the serrated plates are to be seen clearly.

Since these plates in all the species of *Aedes*, *Culiseta*, and *Culex*, that were examined stain light red basally and dark red to orange distally, they are quite hard. This is understandable because the mandibular teeth which are of similar hardness strike against them. The hardness of both structures could be felt with dissecting needles. In the *Aedes* species a group of broad, apically serrated hairs originates on the midventral side of the premental lobe. Broad, but not serrated hairs occur in the same position in the *Culiseta* and *Culex* species. These hairs are numerous in *Aedes* and *Culiseta* but very scarce in *Culex*. In all the species examined they stained medium red with Mallory's.

On the premental lobe laterally, between the central and the lateral serrated plates four small papillae are present on each side in all the species of *Aedes*, *Culiseta*, and *Culex* that I examined. The most

posterior papillae are double on each side; the more anterior two arise singly. Two similar papilla-like processes are present in the membrane dorsally between the serrated plates and the salivary duct opening. In all the species considered the papillary structures stained red, and the basal membranes light blue. In feeding larvae, food often collected in the spaces between the papillae and the serrated plates.

It is difficult to homologize the structures of the labium because of its degenerate nature, but since a pair of muscles attaches the rectangular lobe to the subgena medially to the posterior tentorial pits (fig. 1), these muscles are considered as the premental muscles by Cook (1944b, 1949), Snodgrass (1959), and others, Snodgrass refers to the lobe as the labial plate. I agree with Cook in calling it the prementum.

The premental membrane is dorsally suspended from the hypopharyngeal bars. A weak suture continues between these bars and dorsally of the premental membrane, thus demarcating an oval membranous hypopharyngeal area above the prementum. The opening of the salivary duct is located between the premental and hypopharyngeal lobes. This was so in all the species examined including *A. aegypti* although Christophers (1960) shows it in the center of the prementum.

The triangular serrated sclerite below the prementum has been variously named (table 1). I agree with Cook (1944b, 1949) that it represents the submentum. Salem (1931) considered it homologous with the submentum, but thought that the customary name, mentum, should be retained. Snodgrass (1959) believed it to be an extension of the subgena. Jones (1960), following Snodgrass, calls it the hypostomium in the larva of *Anopheles quadrimaculatus*. My main reason for disagreeing is that in all the species examined this sclerite articulates with the subgena, and therefore is unlikely to be an extension of it. Generally the submentum of insects articulates with the ventral part of the cranium (Snodgrass 1933). Snodgrass (1959) however, does not mention that this triangular structure arcticulates with the subgena. He states that it is continuous with the subgena, as in the head of *Chironomus* described by Grouin (1959) who calls it the hypochilum. Miall and Hammond (1891) indicate that this plate in *Chironomus* seems to correspond to the submentum of orthopterous insects.

The submentum stains orange basally with Mallory's and remains dark brown apically in all the *Aedes*, *Culex*, and *Culiseta* larvae I examined. It is thus a very hard structure. In the species examined the number of serrations on it in mature larvae is usually constant; data are given in table 2.

The lightly sclei otized fringe of hairs (figs. 1, 2) attached to the submentum ventrally stains similarly; I consider it a part of the submentum since it is very intimately connected with this structure. Cook (1944b) calls it the aulaeum.

The Pharynx

The structure and musculature of the pharynx of *A. fitchii* and *C. inornata* larvae are similar to those of *Theobaldia incidens* (= *Culiseta incidens*) described by Cook (1944b). The large dorsal and ventral sclerites stain light orange in all the *Aedes*, *Culex*, and *Culiseta* larvae

TABLE 2 - The numbers of serrations on the submentum of the larvae
of mosquito species.

Species	No. of submental serrations		Species	No. of submental serrations	
Aedes spp.			*Aedes* spp.		
campestris	27. 0	(1)*	sticticus	21.6±0.5	(3)
canadensis	20. 0	(1)	stimulans	28.0	(1)
cinereus	25. 0	(1)	vexans	26.0±0.7	(5)
excrucians	20.5	(2)	*Culiseta* spp.		
fitchii	20.6±0.9	(20)	impatiens	25.0	(1)
hexodontus	24.6±1.1	(5)	incidens	18.0	(1)
implicatus	18.0	(1)	inornata	23.9±2.2	(17)
increpitus	25.0	(1)	morsitans	19.0	(2)
impiger	20.5±1.3	(4)	*Culex* spp.		
pionips	24.0	(2)	pipiens	21.0	(2)
punctor	27.1±0.7	(6)	tarsalis	13.0	(2)
riparius	23.0±0.7	(5)	territans	13.0	(2)

* average ± S. D. of the mean (where applicable);
number of specimens examined in parentheses.

examined. The lateral dorsal hairs stain light red, and the inner filtering hairs stain light blue in most species. Schremmer (1949) described the filtering function of the pharyngeal hairs in *Anopheles maculipennis* larva.

Discussion

It is difficult to decide on the homologies of degenerate structures like the maxilla and labium of mosquito larvae. Shalaby's (1957d) interpretation of the triangular labial sclerite as the paraglossa, and the aulaeum as the glossa is unique, and seems unreasonable. The areas which I consider as the hypopharynx and the prementum Shalaby regards as the hypopharynx. Medio-laterally on the premental lobe a pair of muscles is inserted. These muscles originate on the ventral sclerite of the head which Shalaby considers as the submentum and which I regard as the subgena. It is difficult to agree with Shalaby's interpretation of the labium and the hypopharynx for the following reasons: firstly, as far as is known, the hypopharynx in insects is not connected with the paraglossa, but in the mosquito larva, in Shalaby's interpretation the " hypopharynx " is firmly attached to the "paraglossa". Secondly, other authorities on the morphology of insect larvae (Cook 1944, 1949; Hinton 1958) state that the retractor muscles of the hypopharynx are absent in Diptera. Thirdly, when the retractors of the hypopharynx are present they arise on the postoccipital ridge in the Trichoptera, and on the tentorial bridge in the Lepidoptera (Hinton 1958), but not on the "submentum" where these muscles originate in the mosquito larva according to Shalaby's interpretation.

Very few muscles which could serve as guides to homology are present, and this is partly why disagreements exist among the various morphologists who have studied mosquito larval mouthparts. Ferris (1948) postulates the following principle: ".....the evolutionary changes are first to be accounted for by modifications of pre-existing structures, or by loss of pre-existing structures;..... Only after these possibilities have been exhausted will we assume that a completely new structure has been developed...." This principle can be applied to mosquito larvae and to the larvae of other primitive Nematocera when we compare them with panorpoid larvae. In mosquito larvae noticeable modification from *Panorpa* is seen in the labrum and in the mandibular teeth. Losses and fusions of pre-existing structures are evident in the mosquito larval maxilla and the labium.

A difference was found in the hardness and flexibility of the cuticle of the mouthparts of the filter feeding, browsing, and predatory mosquito larvae. Essentially, the mouthparts of the filter feeders are rather soft except for the labral brush hairs and the mandibular teeth; the mouthparts of the browsers are harder, and the mouthparts of the predatory larvae are the hardest of all, especially the mandibles, which are highly sclerotized.

The tips of the simple labral brush hairs of the filter feeding and browsing larvae are softer than the main parts of the hairs. The labral brush hairs of these groups of larvae are much harder than they appear to be since they are refractory to stain until after boiling in a relatively strong (8%) solution of KOH. It was interesting to find that

the serrated ends of the lateral labral brush hairs of the browsing larvae stain blue and thus are soft combs rather than hard ones as they might be expected to be when their function is considered. Since they are soft it is probable that when they rub over surfaces soft particles are detached and then directed towards the mouth. The physical characteristics of the cuticle were estimated by manipulating the mouthparts, and the impressions obtained agreed with the indications from staining.

The serial row attachment of the labral brush hairs to their respective bars is similar in the browsing and the filter feeding larvae. Christophers (1960) also noted that the hair attachment is similar in the larvae of a *Culex* species and of *A. aegypti* .

In table 3 it is indicated that a reduction occurs in the numbers of hairs or bristles on the various mouthparts from the filter feeders to the predators. In the same series an increase in the sclerotization of the mandibular teeth is evident.

TABLE 3 - Similarities and differences in the mouthparts of filter feeding, browsing, and predatory mosquito larvae.

	Labral brush hairs	Maxillary hairs	Premental hairs		Mandible	
				Sclerotization		Plane of action
Filter feeders						
C. morsitans	many long thin simple	many very long	few short	moderate	slight	
Intermed.						
Aedes cinereus	many thin simple	very many long	many long	moderate	heavy	nearly dorso- ventral
Browsers						
Aedes fitchii	many thick serrated	very many long	many long	moderate	heavy	
Culiseta inornata	many thick serrated	few short	many long	moderate	heavy	
Predators						
Mochlonyx velutinus	few short thick serrated	very few very short	many mostly long	slight	very heavy	antero- lateral
Chaoborus americanus	very few thick short serrated	none	very few short	none	very heavy	

It is interesting to note that the same genus is represented by filter feeding (*Culiseta morsitans*) and browsing larvae (*C. inornata* and *C. impatiens*) whose mouthparts tend towards the predatory type. Most

of the *Aedes* species that were studied are browsers, but the larvae of *Aedes cinereus* Meig. and *A. canadensis* lack serrations on their labral brushes, have more weakly sclerotized mandibular teeth than the other *Aedes* species, and their maxillae are similar to those of the filter feeders. Thus morphologically these species seem to be intermediate between the filter feeders and the browsers.

From table 3 it is also evident that the plane of action of the mandibles in the predatory larvae tends towards that of the longitudinal axis of the body which is a character common both among the larvae of the higher flies, according to Cook (1949), and among predators generally.

FUNCTION OF THE MOUTHPARTS OF MOSQUITO LARVAE

Procedures

The movements of the mouthparts of mosquito larvae and actions resulting from these movements were studied in two situations: behaviour of larvae (mostly *Aedes*) was observed in the muskeg pools in the Flatbush area (100 miles north of Edmonton) in the summers of 1960 and 1961; more extensive observations were made on active larvae in artificial containers in the laboratory.

After being collected the larvae were kept in pint glass jars, and in order to retard their development when not being observed they were kept in the refrigerator at 40°F. The larvae were observed in groups and individually in the glass jars and some details of movements of their mouthparts were seen with the aid of a 10X hand lens. Individual larvae were placed in small vials and their mouthparts were observed from the side with a hand lens. A viscous solution of an inert material such as methyl cellulose was also used to slow down the motions of the mouthparts so that details of their actions could be studied.

Larvae of *A. aegypti* and *Culiseta inornata* reared in the laboratory were observed. Other species of *Aedes* and *Culiseta* were collected in the areas of Flatbush, Edmonton, Lake Hastings, Banff, and Seebe, Alberta. The larvae were identified with the keys of Rempel (1953) and Carpenter and La Casse (1955).

Since the mouthparts are ventral it was desirable to observe larvae from the ventral side; three methods were used for this. For all the methods a container was made by cutting a 1 in long piece of a plastic vial of 1 in diameter, and gluing it to a microscope slide which formed the bottom. The container was filled with either pond water or distilled water and food was added. Usually one larva was studied at a time, but sometimes two were observed in the same dish.

By means of two concave mirrors, light from two microscope lamps was directed on the larva through the bottom of the container. An image of the ventral surface of the larva was reflected by two plane mirrors at 45°, one below the container and one below the objective of a stereo-binocular microscope. A satisfactory view of the mouthpart

movements was obtained in this apparatus. The movements were most clearly seen at magnifications of six or twelve diameters. More detail was seen under 25X and 50X, but the images were blurred, especially at 50X.

A second method of observing the mouthparts was by turning the body and eyepiece of the binocular microscope upside down and focussing on the larva above the microscope. The best image was obtained by this method which was used most often. Fluorescent light from above and focussed light from below were used separately and in combination.

A third and most convenient method of observing the movements of larval mouthparts was through a metallurgical binocular microscope with the stage above the objective lens. In this method it was possible to have the light coming only from above.

Particles of activated charcoal or methyl red were placed in the containers with the larvae to show the directions of the currents set up by the mouthparts.

Observation of the Mouthparts in Action

The operation of the lateral labral brushes was studied by direct observation of living larvae and by manipulation of prepared material. The mechanism of action in each type of mouthpart is described separately below.

Browsers

In this group contraction of the labral muscles exerts tension on the brush sclerite which in turn pulls the tessellated membrane and the cross bars by their hooks. This causes the hairs of the brush to move ventro-medially. The hairs spring back outwardly through the elasticity of the tessellated membrane. The inward and outward movement of the hairs is thus caused by the differential elasticity of the tessellated membrane and the cross bars. The bases of the hairs are connected with the cross bars, and fork on either side of them (fig. 5). The bifurcations are short, and their ends terminate in the tessellated membrane below the cross bars. The stretch of the tessellated membrane allows the part of the hair which is attached to the rigid cross bar to move more than the tips of the fork, so that the hair pivots about this attachment to the cross bar, and its tip swings ventro-medially. Relaxation of the labral muscles allows the hairs to return to their original positions through the elasticity of the tessellated membrane.

The angle through which a hair swings should increase with its distance from the brush sclerite since it is separated from this by a greater length of the elastic membrane. This would have the effect of bunching the hairs together in the median position and allowing them to fan out in the lateral position, which was repeatedly observed to happen.

The main feeding current, produced by the lateral labral brushes, is directed toward the epipharynx and the mouth by the median labral brushes. When creating a current the lateral labral brushes vibrate from

TABLE 4 - Mean frequency and duration of movements of the lateral labral brushes of larvae over one minute periods at 24 to 27°C.

Time in min.	4th instar means of 3 larvae		2nd and 3rd instars means of 4 larvae		4th instar means of 3 larvae	
	Cycles per sec.	Average duration sec.	Cycles per sec.	Average duration sec.	Cycles per sec.	Average duration sec.
5th	1.7	28.5	2.6	11.0	2.0	30.0
10th	2.7	17.7	3.0	11.0	3.3	13.0
15th	3.3	37.0	2.4	62.5	1.8	8.0
20th	3.1	35.5	3.1	24.0	1.8	7.0
25th	3.4	65.0	2.8	16.4	1.8	7.0
30th	3.5	27.0	2.6	31.0	1.8	4.0
35th	4.0	25.0	3.0	11.7		
40th	3.7	36.4	2.8	12.0		
45th	3.6	68.0	2.1	6.0		
50th	4.5	32.5	4.6	13.7		
55th	3.7	61.0	3.2	12.5		
60th	3.5	40.3	3.4	16.6		

postero-medially to antero-laterally. The brushes of *A. aegypti* may vibrate for as long as 2.5 min without stopping. Then they usually stop for 5 - 10 sec before resuming. The more usual timing is vibration for 50 sec, stop for 5-10 sec. and then vibration again. In *Culiseta inornata* and in the browsing *Aedes* species the duration of movement is shorter. Frequency and duration of movements for *C. inornata* and *A. aegypti* and indicated in table 4. Table 5 shows activity of individual 4th instar *C. inornata* larvae, each of which was observed for 30 minutes. During each 30 minute period the activity of the whole body and of the mouthparts. was observed, and the percentage of time spent in each observable activity was calculated.

Feeding and locomotory activities of approximately 50 *C. inornata* larvae were observed individually for various periods of time throughout the period of the study, and many more were observed in group behaviour. Much similarity was noticed in the pattern of behaviour of the various individuals, and almost any larva could be chosen to represent the common sequence of activities. The following is a summary of the activities of a 4th instar *C. inornata* actively browsing larva (no. 6 in table 5), observed for 20 min at a magnification of 25X. The container was filled with pond water.

During the first minute the larva was stationary; it was suspended from the water-surface with labral brushes extended. For the next 10 sec the labral brushes, the maxillae, and the mandibles created a current, then a 10 sec period of rest followed with the mouthparts retracted and the whole body still. During the first 5 min period such a succession of currents in which all the mouthparts participated was produced four times, and each time the labral brushes moved about 15 times. The mandibles and the maxillary brushes also moved approximately as many times as the labral brushes.

TABLE 5 - Percentage of time spent by 4th instar *C. inornata* larvae in different activity states over a 30 min period.

Body of larva		Labral brushes		
Stationary	Moving	Retracted	Extended	Moving
48	52	37	48	15
52	48	18	59	23
62	38	22	57	21
44	56	0	63	37
53	47	6	25	69
12	88	35	29	36
45	55	5	16	79

The larva browsed on a filamentous piece of plant for ten seconds. The piece of plant was enclosed by the labral brushes and the mandibular teeth struck it. Then the larva moved to a chickweed leaf and browsed on its edges for 18 sec. The median hairs (type 3) of the lateral labral brushes held the edges of the tissue while the more lateral hairs (type 3) of the brushes produced a current which moved the larva forward along the leaf. The mandibular teeth struck the tissue. Then the tissue was left and further currents were produced by the mouthparts. Pieces of debris passed into the current which was produced continuously for approximately 20 sec. Mandibular teeth chopped off small pieces of decayed material, some of which went into the mouth and the remainder moved out with the current. Again a piece of plant tissue was browsed upon, and was then propelled posteriorly. When one end of the plant was at the submentum the aulaeum clung to it for a few seconds, but with the subsequent current the tissue was forced posteriorly and towards the bottom of the container.

During the next ten minutes continuous movements of the mouthparts occurred 15 times, each time the duration of the current was approximately 15 sec.

The amount of brush movement and body movement varies among larvae of different ages and different species. Fourth instar larvae are more sluggish than younger ones, and 4th instar *Culiseta inornata* and *Aedes fitchii* larvae are more sluggish than the corresponding instars

of *A. aegypti* (table 4). Shannon (1931) and Christophers (1960) also noticed that *A. aegypti* larvae moved considerably faster than the larvae of most other species of mosquitoes. Fourth instar *A. aegypti* larvae can ingest charcoal particles faster than 4th instar *C. inornata* larvae. When activated charcoal was placed in a container with 3 *A. aegypti* larvae and in another container with 3 *C. inornata* larvae (all 4th instar), the guts of the former were filled in from 90 to 105 min, whereas the guts of the latter species were only filled after 3.5 hr. Larvae of all the species observed moved faster and more frequently when they were stimulated to activity by other organisms (*Daphnia*, *Cyclops* etc.).

When the brushes are not rhythmically beating to create a feeding or a locomotory current they remain extended and separated into rows of four or five layers (fig. 7), or they are retracted (fig. 7). Particles which have been brought close to the mouth by the current continue streaming towards the mouth through the spaces between the rows of hairs, or if the brushes are retracted the particles come to rest on the maxillary brushes. If these are extended the particles stream into the mouth and some settle on the hairs of the pharynx, the mandibles, the maxillae and the prementum. The separation of the labral brush hairs into several rows (fig.7) is possible because of the basal structure of the brush. Each row of hairs can be moved about the axis of its cross bar. Several rows can move in one direction together, and thus water can flow through the spaces between these groups of hairs. It also seems that the water currents can force the labral brushes to close. The muscles that insert on the tormal apodemes (fig. 3) extend the brushes by contraction. Relaxation of the labral muscles allows the hairs to return to their original positions through the elasticity of the tessellated membrane. This can be demonstrated in preserved specimens. The contraction of these muscles and of the epipharyngeal muscles was observed in living larvae of a filter feeder, *Culiseta morsitans*.

The feeding currents of *Aedes* and *Culiseta* browsers are fast and can carry large as well as small particles. Objects about one third the size of a larval head can be circulated in the stream (fig. 8), the current and the particles reach as far posteriorly as the fourth and fifth abdominal segments and extend about the same distance in front of the larva. Such circulation of particles can be observed when the larva is suspended in water and also when it lies on its dorsal side in an observation cell.

When a larva feeds just above a loose sediment (fig. 8) or browses its way forward through debris in a container, the particles that do not enter the mouth fall to the bottom of the container or cling to the brushes; they do not return to the feeding current. The feeding current is effective only in front of the larva, and it is slowed down behind the larval head. The water flows ventrally rather than posteriorly below the body of the larva. When the larva leaves the browsing area many particles remain on its labral and maxillary brushes, since what does not fall to the bottom of the container sticks to the brushes. Some filtering is done by the labral brushes, especially by the median serrated ends of the lateral labral brush hairs, quite large particles are found clinging to them. Since particles only slightly smaller than these have been found in the pharynx and in the intestine, and since most food seems to come into the mouth via the

labral brush current, it seems reasonable to assume that the particles which passed into the mouth and eventually into the gut were filtered out by the brushes. The serrated brush hairs are useful in browsing, for as they move along surfaces they detach particles from them, many of which are consumed.

With its labral brushes a browsing larva can attach itself to a grass stem, to the side of a container, or to a body of a pupa or another larva. While the labral brushes cling to surfaces the maxillary brushes produce a current. The browser's maxillary brushes can create currents that are as strong as those of the labral brushes. This was observed in fourth instar larvae of the following species:*Aedes cataphylla*Dyar,*A. sticticus*(Meigen), *A. communis* (De Geer),*A. fitchii ,A. punctor,A. riparius,A. canadensis , Culiseta inornata* and *C. impatiens .* The larvae can also browse on parts of their own body, especially on the posterior regions of the abdomen. This was observed particularly in containers where *Aedes* and *Culiseta* larvae were crowded. Many times larvae, especially *C. inornata* and *Aedes canadensis .*, were seen browsing on the tips of their own abdomens and creating currents at the same time. They were in loop-like positions and moved in circulating paths of the water surface. This was particularly notice-able in the laboratory with the larvae of *A. canadensis*; on one occasion in June 1960, 20 to 30 larvae turned in this manner for several minutes, individual larvae turning for as long as five to six minutes. Christophers (1960) states that larvae browse on parts of their own bodies, especially on the posterior parts, when they are starving. My observations agree, for in situations where this behaviour took place little food was present.

Interfacial feeding (Renn 1941, and fig. 8) is a common method of feeding in the *Anopheles* filter feeding larvae. Third and fourth instar *C. inornata , A. aegypti , A. fitchii , A. punctor ,* and *A. riparius* larvae also brow-sed at the water surface without browsing on their siphons at the same time. In this second type of filter feeding only the head of the larva was at the water surface and the rest of the body remained under water.

In most browsing activities all or most of the mouthparts are employed. When an object such as a long thin piece of decaying grass comes into the feeding current, it comes in contact with the mouthparts as follows:firstly, the serrated lateral labral brush hairs (median type 3) hold a part of it, and push the remainder posteriorly; second, it slides over the central labral brush; third, it passes between the epipharyngeal bristles; fourth, the mandibular denticles strike it as it passes by, and if a small piece of it is thus torn off it may go posteriorly with the current, it may be drawn into the mouth, or it may settle on the prementum; fifth, it passes between the maxillary brushes; sixth and finally, the particle of grass touches the submentum and the aulaeum. During this process some of the median labral brush hairs hold the particle while the remaining hairs of the brush produce currents.

Sometimes parts of the lateral labral brushes move only slightly (median type 3 hairs) whereas the hairs of their most posterior (types 2 and 3) move more actively. More commonly, all the hairs on the brushes move simultaneously when producing a current. When a larva comes to a stop after moving about in a container, it will gradually extend

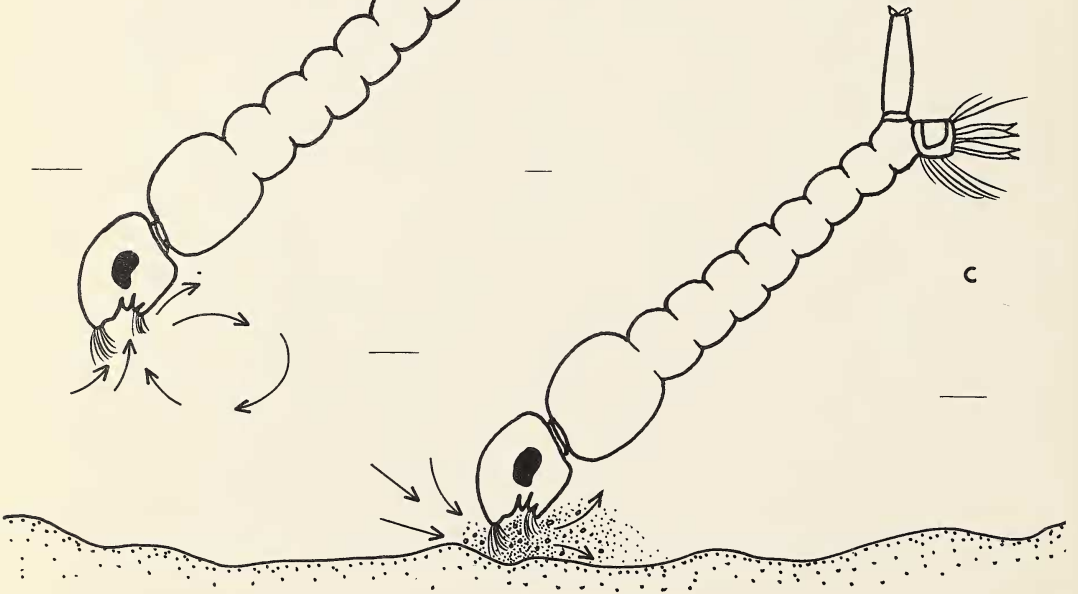surface view of currents
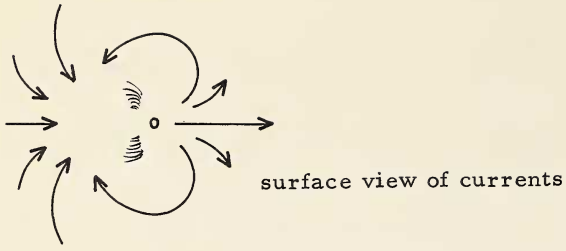
labral brush   maxillary brush

a
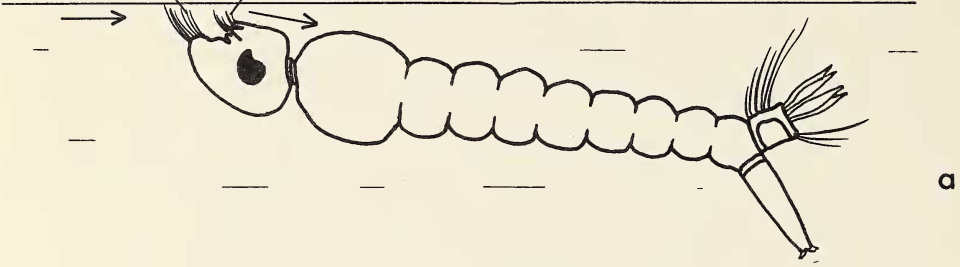
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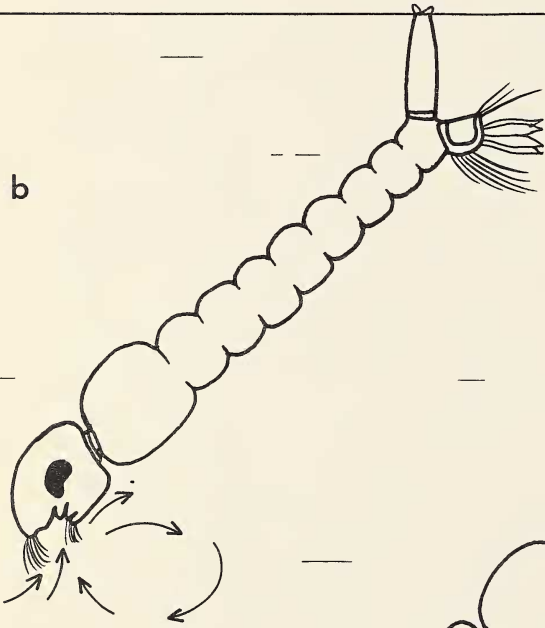
c

Fig. 8. Movements of labral brush currents of browsing larvae; (a) interfacial surface feeding current, (b) current produced under the water surface, (c) current used to stir up debris from the bottom.

or contract the brushes.

Most of the observations on the coordination of moving mouthparts were on *Aedes aegypti* and *A. fitchii* larvae which had been slowed down in a 20 to 30% solution of methocel of 400 centipoises. The larvae were watched in white porcelain spot plates with their ventral sides turned up. The following combinations of mouthparts were observed in action: 1. The lateral labral brushes moved in their usual antero-posterior oblique direction, and the long apical setae of both maxillae moved backwards and forwards at the same time. 2. The lateral brushes moved in their usual direction while the setae of one maxilla remained stationary, directed posteriorly, and the setae of the other maxilla continued their antero-posterior motion. The epipharyngeal bars also moved. 3. The lateral labral brushes were motionless. At the same time either one or both maxillary brushes waved and thus kept the current in motion. 4. The lateral labral brushes came to rest on the epipharynx and at the same time the other mouthparts moved in one of the following ways: one or both maxillae moved in the transverse plane; one or both mandibles moved in the transverse plane, striking against the hypopharynx; or, one mandible and one maxilla on the same or the opposite side moved. The same type of combination of mouthpart movements was observed in the larvae of the following species: *Aedes cataphylla, A. excrucians ,Aedes fitchii, A. hexodontus* Dyar, *A. punctor , A. riparius, A. sticticus , A. vexans ,* and *Culiseta inornata.*

Aedes aegypti larvae also browsed on poplar and elm leaves in the laboratory. For two weeks ten larvae were given no other food but dried leaves of *Ulmus* sp. and no mortality occurred. At the end of the two week period all the larvae had pupated. The larvae of this species are also reared on leaves of a species of poplar in South Africa (Hocking, personal communication).

Browsing larvae of *Aedes* and *Culiseta* were observed in deep water pools (approximately 1. 5 to 2. 5 ft. deep) and in shallow pools (four to 12 in. deep). In shallow pools with clear water it was possible to see larvae browsing on submerged rotting leaves and other objects for as long as three minutes without coming to the surface for air. When the larvae came to the surface they sometimes remained there for one to five minutes and they either moved slowly or continued in one position before submerging again. Sometimes the wind disturbed the surface of the pool and some of the larvae that were at the surface moved with the wind, while others swam against this. In situations of this type, however, most larvae went to the edge of the pool, where a stable resting position was found.

Several observations of larval activity were made at a pool 1. 5-2 ft. deep, and the courses of larval movements were recorded. *Aedes excrucians* and *Culiseta inornata* larvae were able to remain in a stationary position at the surface for from a few seconds to four minutes. During this time they probably produced currents with their mouthparts as did the larvae of these and other browsers when observed in a glass container in the laboratory. The approximate mean distance that any one larva covered in four minutes was between four and five feet. In a larger pool some larvae covered more space than this before submerging. The larvae went under either of their own accord, or wehn they came in contact with

another animal in the water such as a snail, a water beetle, a crustacean, or a dead insect floating on the surface. When larvae submerged without coming in contact with something first, after detaching their siphons from the surface film, they were pulled downward by the currents of their mouthparts.

In pools populated with browsing larvae and located in areas which were partly shaded, the shaded areas were much more crowded with resting larvae, although the sunny areas were used for moving about and browsing by a few larvae. This behaviour can be interpreted as orthokinetic (Fraenkel and Gunn 1960).

Filter Feeders

Three filter feeding species are at present known in Alberta, representing three genera; *Anopheles earlei* Vargas, *Culiseta morsitans*, and *Culex territans* . All of these species are uncommon, hence it was not possible to study the morphology and function of the mouthparts of their larvae in much detail.

Feeding larvae of *Anopheles earlei* were observed in the laboratory , but most were reared into adults and none was preserved for morphological study. *Anopheles earlei* larvae are small and are usually found in deep water, hence it is difficult to observe the action of their mouthparts in their natural habitat. In the laboratory all were usually at the water surface It was common to see some larvae resting with parts of the abdomen or thorax or both against the side of the container, while others moved in circular paths around the container. Often two or three larvae moved side by side in one direction, while one or more other larvae moved in an opposite direction. Sometimes two larvae, moving towards each other, collided and then both moved together in the direction initially travelled by one or the other. It is not known what determined the final direction of movement; perhaps the larva producing the stronger current overrode the other. *Anopheles* larvae turned their heads through 180 degrees so that the ventral side of the head was at the surface for period of 25 to 30 sec at a time as compared with approximately 10 sec periods in the normal position.

According to Clements (1963), The area of surface that can be cleared of particles by an *Anopheles* larva in a given time varies with the size of the larva, density of particles, and the rate of filtration, which is affected by temperature. The effect of these factors on larval movement was not considered in this study.

The movements and feeding behaviour of *Culex territans* and *Culiseta morsitans* are similar. The two species are found in the same type of habitat, and their mouthparts are similar in form. Since the labral brushes in these species are longer than in the *Aedes* or *Culiseta* browsers, the currents they create cover a larger area than do those of the browsers. Also these filter feeders extend their labral brushes mainly laterally, whereas the browsers extend theirs antero-laterally. Several *Culiseta morsitans* larvae were observed in a glass jar in the laboratory. They moved rapidly by means of the labral currents and fed at the same time; the pharyngeal movements could be seen through the head cuticle. Sometimes minute crustaceans were brought to the mouth with the current,

but they were not ingested. The food of the larvae consisted mainly of moss particles which floated in the pool water, and settled on the bottom of the jar. The particles on the bottom of the jar were agitated by browsing *Aedes cinereus* or *Culiseta inornata* larvae often collected with *C. morsitans*. Occasionally the *C. morsitans* moved their labral brushes just above the sedimented particles on the floor of the jar in the same manner as the browsing species. Sometimes two, three, or more of these filter feeding larvae rested in one location close to each other, clinging to the water surface film with their siphons, and moving their labral brushes. Most frequently the larvae stayed in such a position between two and three minutes before being disturbed by a moving larva or crustacean. When disturbed, the larvae either submerged, or moved horizontally on the water surface to another location. The first course was followed by about two thirds of the larvae. After submerging, each larva went in a different direction and stayed under the water surface for 10 to 15 sec. Upon coming to the surface the larvae either resumed their stationary positions for two to three minutes or until disturbed, or they moved horizontally, propelling themselves by the feeding current. In submerging when disturbed and in returning to the water surface the characteristic wriggling motion of the abdomen was used.

In the laboratory *C. morsitans* larvae assembled in the shady rather than the sunny part of a container. This observation is in agreement with that of Hocking (1953) on *Aedes communis*.

Predators

Three species of predatory larvae, *Chaoborus americanus*, *Mochlonyx velutinus*, *Eucorethra underwoodi* Underwood were collected near Flatbush, Alberta during the summers 1960 and 1961. *C. americanus* larvae were observed feeding on the larvae of several species of *Aedes* in the laboratory. The feeding behaviour of *Chaoborus* species has been studied in detail by Montchadsky (1945) and by Schremmer (1950). Both authors discussed the modification of the larval mouthparts for their predatory function. The mandibles in the larvae of this genus are the important movable mouthparts. The maxillae are fused with the ventral part of the cranium, and prementum is reduced to a wedge-like plate. The mandibles do not have a primarily crushing function, but their sharp strongly chitinized teeth have a holding and pushing function (Schremmer 1950). These larvae also use their prehensile antennae for catching prey. They ingest their prey whole. The main features of the mouthparts of *Chaoborus americanus* are indicated in table 3. The posterior occipital parts of the head capsule of *Chaoborus* larvae are connected to the subgena by membranes (Cook 1956); this permits the mouth opening to become enlarged whenever necessary.

In *Mochlonyx velutinus* larva the ventral part of the head is sclerotized, but a large mouth opening is present, as the head capsule is wider than in *Chaoborus*. Cannibalism was observed among the *M. velutinus* larvae in a jar in the laboratory. The raptorial function of the mandibles and antennae was observed when the larvae caught their prey tail first. Then the prey seemed to be held by the maxillae while the mandibles continued striking it and pushing it further into the mouth. In the specimens that I observed the process of ingestion lasted approximately two hours.

Digestion may take as long as three hours (Montchadsky 1945). Some-
times a feeding larva lost its prey, even if this was half ingested, if it
was disturbed by other organisms. James (1957) observed that *M. velutinus*
larvae are occasional predators on other mosquito larvae. I observed
M. velutinus feeding on larvae of various *Aedes* species. A similar habit
was observed in *M. culiciformis* De Geer by Montchadsky (1953) and
Montchadsky and Berzina (1959). Cannibalism was also observed in
Cryophila lapponica Mart. by Montchadsky (1953).

Discussion

The larvae that I studied in this investigation can be classified
as filter feeders, browsers, and predators. There are more similarities in
the structure and in the function of the various mouthparts of filter feeders
and browsers than between either one of these types and the predators.

The labral brushes of filter feeders and browsers are used for
bringing food to the larvae by means of currents which they produce by
vibrations. By means of these vibrations the larvae also move through the
water. The labral brushes of the predatory larvae are reduced to a few
bristles and do not produce currents.

The epipharynx of the browsing and filter feeding larvae is believed
to have the function of covering the mouth opening (Schremmer 1950).
This was not observed in the larvae that were studied in this project.
The epipharyngeal hairs were erected by the muscle which moves the
epipharyngeal bar, and when these hairs came in contact with the labral
brush hairs, food from the brush hairs was transferred to them. The
epipharyngeal hairs were in turn scraped by the mandibular hairs, and
this food was thus passed towards the mouth opening. If the food did not
go into the mouth, as often happened, particles of it remained on the pre-
mentum and on the hairs of the lacinia.

Mandibles of the browsing larvae were observed in actions of biting
while the larvae browsed. Those of predators were seen grasping and
pushing the captured prey into the mouth. The mandibles of the filter
feeders and the browsers move in a dorso-ventral plane, but those of
the predators move in an oblique plane which is nearly parallel to the long-
itudinal axis of the body.

LARVAL FOOD AND MOUTHPARTS

As a final step in investigating the function of the mouthparts the
nature of the food of the functional groups of larvae and the relationship
between the size of the food particles and the dimensions of the mouth-
parts were studied.

Procedures

The gut contents of several species of *Aedes*, *Culiseta*, and *Culex* lar-
vae were examined and measured. Most of these contents were dissected
out and mounted in glycerine jelly, a suitable preservative for plant mater-

ials (Sass 1940). Particles of activated charcoal were made available to sev-
eral *A. fitchii* and *C. inornata* larvae, and ingested as well as uningested
particles were measured.

The following measurements were taken of the larvae of available
species,including *Anopheles*, *Chaoborus* , and *Mochlonyx*:   head width (between
the bases of the antennae), head length (between the median labral brush
and the occiput), mean length of the right lateral labral brush (at the center
of the brush), width of the right lateral labral brush (width at the
base of the brush), and the width of the epipharyngeal constriction (space
between the most posterior, longest teeth on the transverse bars of the
epipharynx).

An examination was also made of the material suspended in the
water of a larval habitat. Ten litres of water was taken from a pool near
Edmonton where *C. inornata* larvae were collected in   September, 1961.
This water was passed through a series of sieves. Material that did not
go through the first sieve was examined, and a rough estimate of its comp-
osition was made. These fractions of material were then dried at $100°C$
to constant weight;they were ashed in a muffle oven at $575°C$; the ash was
weighed and the percentage loss was calculated.

Results

Table 6 contains a summary of the sizes of particles that were found
in the guts and in the environment of the larvae of *Aedes fitchii*, *Culiseta inornata*
and *Culex territans* . Particles that were identified from the guts of 4th
instar larvae of these species are listed in table 7. From this
table it is seen that the gut contents in the three species were similar.

The relationship between the structure of some mouthparts and
the feeding habits of larvae is shown in fig. 9. The points on the graph
were derived in the following manner:(1) for the position on the abscissa
the mean length of the right labral brush was multiplied by its mean width
to give the area swept by the brush. This product was divided by the pro-
duct of the head lenght and the head width, to relate this to the size of the
larva. (2) for the position on the ordinate the width of the epipharyngeal
constriction was divided by the head width to represent the maximum
relative size of particles which could be swallowed. Each point represents
the mean value for a species. A separation between filter feeders and
browsers is shown on this graph.

In fig. 9 the intermediates fall closer to the browsers than to the
filter feeders. Typical filter feeders may be tentatively defined as larvae
in which both the ratio of the epipharyngeal constriction to the head width
and the relative area swept by the lateral labral brushes exceed 0.14.   In
browsers and intermediates both of these ratios are less than 0.14. I n
typical predators the first ratio is more than 0.14, but the second is less.
On the basis of morphology representatives of all types of feeders fall
within the range of browsers.

From table 7 it is seen that the gut contents were similar in the
three species, *Aedes fitchii* , *Culiseta inornata* , and *Culex territans* . The guts of
a few *Chaoborus americanus* larvae that were examined were filled with mus-
cle tissue; some of this was from other mosquito larvae.

TABLE 6 - Size ranges of particles in the guts and in the environments of 4th instar mosquito larvae. Percentage by number.

Max. linear dimension in microns	*Aedes fitchii* Charcoal in Water	Gut	*Culiseta inornata* Nat. food in gut	Natural food in Water	Gut	*Culex territans* Charcoal in Gut	Nat. food in gut
< 7.5	4.3	6.1	3.1	2.7	4.0	4.0	12.0
- 9.9	7.2	10.2	7.4	9.8	5.7	8.2	35.4
- 14.9	29.5	31.7	6.3	6.0	10.1	27.1	40.1
- 19.9	11.1	10.0	27.2	35.6	30.3	9.1	7.2
- 24.9	9.0	8.0	11.5	9.0	12.0	9.5	6.3
- 29.9	13.0	9.8	9.3	10.0	11.7	12.2	
- 34.9	6.0	9.2	13.6	11.0	6.2	9.4	
- 39.9	4.9	5.6	10.1	8.5	4.0	3.9	
- 44.9	11.0	5.0	6.7	6.0	5.0	10.0	
- 71	5.0	4.0	5.3	2.0	10.0	8.0	
Nos of measurements	500	500	400	120	500	500	300

TABLE 7 - Organic particles in larval habitat and gut contents of 4th instar larvae of *Culiseta*, *Aedes*, and *Culex*; x scarce, xx common, xxx abundant, xxxx very abundant.

	Culiseta inornata Habitat	Gut	*Aedes fitchii* Gut	*Culex territans* Gut
Diatoms				
Fragilaria sp.	xx	xx	xx	
Gomphonema sp.	xx	xx	xx	
Navicula sp.	xx	xxxx	xx	
Pinnularia sp.		xx	xx	
Stauroneis sp.	xx	xx		
Green Algae				
Ankistrodesmus sp.	xx		xx	
Geminella sp.	xx	xx	xx	
Microspora sp.	xx		xxx	
Scenedesmus sp.	xx		xx	
Spirogyra sp.	xxxx	xx	xx	
Blue Green Algae				
Anabaena sp.			xx	
Gleocapsa sp.		xx		
Fungi				
Cladosporium spores	xx	xx	xx	
Rust - telospores		xx	xx	xx

Fungi				
Rust - uredospores		xx		
Smut spores	xx	xx	xx	xx
Fungi Imperfecti, hyphae		xx		
Pollen of:				
Pinus				xx
Populus	xx	xx	xx	
Compositae	xx	xx	xx	xx
Plant Fibers				
xylem	xx	xx	xx	xx
tracheids	xx	xx	xx	xx
Flagellates				
Chlamydomonas sp.		x		
Euglena sp.	xx	xx alive		
Phacus sp.	xxx	xx alive		
Arthropod material				
Pieces of cuticle	xx	xx	xx	
Larval culicine				
spines, hairs	xx	xx	xx	

TABLE 8 - Particle size and weight in mg of suspended matter in 10 l
of water from a pool occupied by *C. inornata* larvae.

Meshes/in		45	80	230
	Passing	45	80	230
	Retained by	45	80	230	325
Dry weight (mg)		26.4	74.8	434.0	156.0
Ash weight (mg)		12.9	49.4	333.0	124.0
% organic matter		50	31	23	20

The following items were retained from the water taken from a
pool were·*C. inornata* larvae were collected by a sieve with 45 meshes
per inch: 60% *Cyclops* sp. and other copepods, alive;20% decaying animal
and plant .material including mosquito eggs, egg cases beetle abdomens,
and mosquito wings; 20% algae, mainly *Spirogyra* sp. The dry and ash
weights and percentage of organic matter in the material held by sieves
of finer mesh are given in table 8.

Discussion

In examining the gut contents of browsing, filter feeding, and pre-
datory larvae it was found that the browsing *Aedes* and *Culiseta* larvae
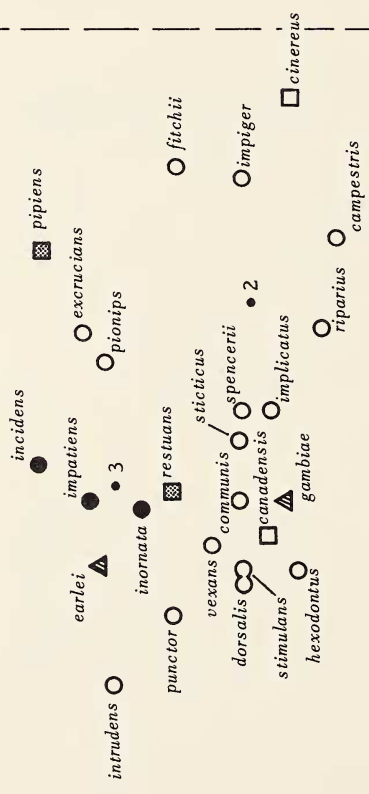ingest items of similar types and sizes. The approximate proportions of

Fig. 9. The relation between feeding habits and morphology of mouthparts of mosquito larvae. ▲ filter feeders, ○ browsers, ☐ intermediates, ✕ predators. Empty *Aedes*, stipple *Culex*, black *Culiseta*, shaded *Anopheles*, 2 & 3, 2nd and 3rd instar *C. inornata* respectively.

the numbers of food particles of the different sizes in the guts of *Aedes fitchii* and *Culiseta inornata* larvae are: less than 15μ, one - sixth, 15 - 22μ, one-third, 22-40μ, one-third, 40-71μ, one-sixth of the measured particles.

In the larvae of *A. fitchii* 58% of the charcoal particles ingested were found to be less than 20 microns with the largest percentage (31.7) in the 10-15μ range; only 6.3% of the natural food particles fell in the 10-15 μ range with the largest percentage (27.2) occurring in the 15-20μ range. A similar relationship was found in *C. inornata* (table 6).

Some plant and animal particles were folded before entering the mouth of the larva. Also when the larvae browsed on plant surfaces they bit pieces off plants, scraped surfaces, and thus obtained soft particles of various sizes and shapes. Many plant particles eaten were long, narrow, and flat, so they were easily carried into the mouth by the feeding current. However, when activated charcoal was placed in the water, the larvae ingested the small particles that were brought to the mouth with the feeding current, but did not take in the large ones which rapidly settled on the bottom of the container. Charcoal particles are denser than natural food and the browsers' currents cannot stir up particles larger than 15 microns. The particles are filtered by the labral brushes; large hard particles are rejected, whereas soft food is actively taken in. Occasionally I stirred the charcoal in the containers. Sometimes the larvae browsed on the bottom of the container, but long, flat particles were difficult to obtain. Thus mostly small charcoal particles were scraped into the mouths.

Since the charcoal particles did not remain in water suspension very long, they were not fed to the filter feeders. Pond food from the guts of these larvae was measured (table 6). Also measured were the spaces between the groups of labral brush hairs through which the feeding current passes. The size of these spaces was found to be similar to that of the particles in the guts. Thus filter feeding is possible among these larvae, for if the ingested particles were larger than the spaces between the hairs, they would not be trapped in the brushes, but would remain on the surface of the brush. On the other hand, very small particles would pass through the brush with the water current without becoming entangled in it.

Also, most of the food particles found in the guts of filter feeders were of the same order of size as the charcoal particles ingested by the browsers, and smaller than the food particles of browsers that fed in the field. The epipharyngeal constriction width in filter feeders is greater than in browsers, therefore it should permit larger particles to pass towards the mouth. However, the mandibular teeth of filter feeders are weakly sclerotized and cannot crush or "squeeze" large particles in the feeding current. Thus large soft particles by-pass the mouth openings of filter feeders, whereas they are pushed into the mouths by the mandibular teeth of browsers. But the wide epipharyngeal space of filter feeders allows the passage of more particles in a given time.

According to Bates (1949), Shipitzina in 1935 found that 4th instar larvae of *Anopheles messeae* Fall. were able to swallow sand particles from 68-165μ wide. The mouth openings of this species must be larger than those of the culicine larvae I studied. The size range of food particles found in the guts of three English species of *Simulium* larvae was found

to be 1.7-15.1μ by Williams *et al* (1961), the size of the mouth openings of these larvae was not given.

McGregor (1963), working with larvae of *Opifex fuscus* found that first instar larvae did not develop serrations on their labral brushes if they were fed on minute particles of dehydrated blood serum. Serrations did develop when they were given fish food ranging in particle size 0.1-0.6 mm. Similar experiments with larvae of other feeding types should be revealing.

The browsing larvae whose guts I examined fed on plant particles and on microscopic animals, whereas the filter feeder *Culex territans* had fed only on plant particles (table 7). Also, all the types of particles that were present in the pool water where the *C. inornata* larvae were collected were found in the intestines of these larvae. It can be said then that these larvae do not discriminate in the type of food they ingest. Other workers have come to similar conclusions: Coggeshall in 1926 as reported by Bates (1949), Howland (1930), and Jones (1960) who worked with anopheline larvae, and Becker (1958) who worked with larvae of *Culicoides circumscriptus* Kieff. These authors have found algae, diatoms, and other plant particles in the guts of *Anopheles* and *Culicoides* larvae. Rempel (1936) found similar food materials in larvae of *Chironomus hyperboreus* Staeg. (= *C. rempelii* Thienemann, Rempel 1962). Other culicine larvae also ingested similar food (Horsfall 1955). Bekker (1938b) found living *Euglena* in the gut of *Anopheles maculipennis*

The *Aedes* and *Culiseta* browsers show similarities in both function and morphology. The range of the ratio of epipharyngeal constriction to head width is from 9 to 12.7, and the ratio of the area swept by the lateral labral brushes to the head size ranges from 4 to 11.8 (fig. 9). Two *Anopheles* filter feeders, one *Aedes* intermediate, and two *Culex* intermediates also fall within these ranges. The second ratio is even higher for another intermediate feeder; it is 13 for *Aedes cinereus*

Of the species I examined, two species of *Culex* and one of *Culiseta* are filter feeders in function and morphology. The species of *Chaoborus* and *Mochlonyx* are predators both functionally and morphologically. The remainder of the species represented in fig. 9 range between these two types either in function, morphology, or both. Thus the *Aedes* and *Culex* species labelled as intermediates obtain their food by filtering, but the structure of their mouthparts is intermediate between the typical filter feeders and typical browsers. The *Anopheles* species are also filter feeders. Their mouthparts fit the general description for filter feeders but the sizes of the mouthparts measured, upon which the division in fig. 9 is based, are proportionately smaller than the sizes of corresponding mouthparts of *Culex* and *Culiseta* filter feeders.

While this method of separating larvae of *Aedes* , *Culex* , and *Culiseta* , into filter feeders and browsers is satisfactory and can be used to categorize the predatory species of *Chaoborus* and *Mochlonyx*; it is not reliable for *Anopheles* . The filter feeding larvae are considered to be the most primitive and the predatory larvae the most advanced (Montchadsky 1937, Surtees 1959). Thus the largest number of the species studied are in a transitional stage of evolution.

GENERAL CONCLUSIONS AND DISCUSSION

According to the functions of the mouthparts three types of mosquito larvae can be recognized: filter feeders, represented in Alberta by *Anopheles earlei* , *Culex territans* , and *Culiseta morsitans*; browsers, including most of the *Aedes* and *Culiseta* species; and predatory, represented by species of *Chaoborus*, *Mochlonyx*, and *Eucorethra*. The *Culex* and *Culiseta* filter feeders are characterized by labral brushes consisting of long, thin, simple hairs, and by lightly sclerotized mandibles. The *Anopheles* larvae have thin, simple lateral labral hairs which are shorter than those of *Culex* and *Culiseta*, slightly sclerotized mandibles, and large rectangular maxillae with short thin hairs. The browsers have shorter labral brushes with some serrated, thick hairs, rectangular maxillae with shorter, thicker brushes, and moderately sclerotized mandibles. The predators bear only a few setae on their reduced labral areas and on their much more fused maxillae, and they have heavily sclerotized mandibles.

Among the browsers morphological intermediates occur. *Aedes canadensis* and *A. cinereus*, have short labral brushes with simple hairs, browser-like mandibles, and maxillae similar to those of the filter feeders. *Culiseta impatiens* and *Culiseta inornata*, have typical browsing labral brushes and mandibles, but have maxillary structures closely related to those of predators.

Not much variation was observed in the structures of the labral brushes, mandibles, or maxillae among most of the browsing *Aedes* larvae studied. However, specific differences were found in the numbers of serrations on the sclerotized plates of the prementum, and on the triangular submentum. These characters may be taxonomically useful.

By staining with Mallory's triple stain it was found that the cuticle of the mouthparts varies in hardness and flexibility. The median hairs of the lateral labral brushes of the browsers have hard basal and central parts, and flexible parts just above the bases, and at the tips.

An examination of larval food revealed that the browsing and filter feeding larvae are not discriminatory in the type of food they accept, but there are limits in the size of particles they can ingest.

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